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WHAT IS AN ADAPTIVE TRAIT?*

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MORPHOLOGICAL CONSERVATISM IN SIBLING SPECIES

The idea of the present article, which attempts to deal with the general problem of the nature of adaptedness of traits which differentiate races, species, and other groups of animals and plants, has been suggested by consideration of a topic apparently not closely related. The genus Drosophila contains a number of pairs, or of groups of several, sibling species. This phenomenon is particularly common among Drosophila of Brazil and of the American tropics in general. Sibling species are morphologically so similar, or nearly identical, that distinguishing them by inspection is difficult or impossible. Yet, they are demonstrably good biological species, since the reproductive isolation between them is complete or nearly so. Why is the genetic differentiation in sibling species not accompanied by morphological divergence?

The quadruplet of sibling species, *Drosophila willistoni, D. paulistorum, D. tropicalis,* and *D. equinoxialis,* may be considered here as an example. Sexual isolation between them is so strong that cross-insemination is rare even when no choice of mates is available; when interspecific copulation does occur no viable progeny is produced. The four species are sympatric over extensive territories in South and Central America; the populations of each species contain arrays of chromosomal variants of the inversion type, but there is no evidence of either regular or occasional transfer of these variants from species to species, as would be expected if effective hybridization occurred, however rarely, in natural habitats. Morphological differences between these species exist, especially in the male genitalia, but they are so slight that it is not feasible to distinguish the species by inspection of living individuals under a binocular microscope, at least not in the female sex (Burla et al. 1949, Spassky unpublished). Analysis of the salivary gland chromosomes shows that the gene arrangements in the

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four species have diverged, especially in one of the chromosomes, the third, which in three of the four species is built so differently that homologous regions are no longer recognizable. There is also good evidence of physiological and ecological divergences. Every species has a distribution area different from the others, as well as habitat preferences of its own. Where the siblings are sympatric they may vary in relative abundance at different seasons. In laboratory cultures, the larval development of *D. willistoni* is faster than that of *D. paulistorum; D. tropicalis* gives beautifully clear polytene chromosomes in the salivary glands, *D. equinoxialis* gives poor chromosomes, while the other two siblings are intermediate.

The reasons for the scanty morphological divergence despite considerable genetic and physiological diversification are a matter of speculation. I have surmised that the external morphology of some species groups of Drosophila has reached so high a level of adaptive specialization that most changes in the visible body structures are discouraged by natural selection; nevertheless, room is left for ecological divergence based on physiological differentiation (Dobzhansky 1941).

Attempts to apply this conjecture to concrete cases lead however to difficulties. Indeed, most of the morphological traits which differentiate related species of Drosophila are of a kind the significance of which for the welfare of the animals is not at all evident. A partial list of these traits will make this point clear: Number of branches in the arista, shape of the facial carina, width of the cheek relative to that of the eye, presence of one vs. two prominent bristles in the oral row, thorax more or less polished or dull, presence or absence and kind of the color pattern on the thorax, number of rows of acrostichal microchaetae on a certain portion of the thorax, anterior scutellar bristles divergent, parallel, or convergent, relative lengths of certain bristles on the pleurae, proportions of certain sections of wing veins, presence or absence and intensity of color markings on the wings, position and kind of bristles on some leg segments, details of the color pattern on the abdomen, shapes of various parts of male genitalia, number of coils in the testes, shape of the spermathecae, number and kind of coils in the ventral seminal receptacle, etc.

ADAPTIVE AND NEUTRAL TRAITS IN CLASSIFICATION

Why should these and other similar traits vary in some species groups of Drosophila, and yet be fixed in species of other groups making the latter sibling species? This problem is only a special case of a more general one, that of the adaptive significance of the keleidoscopic diversity of morphological traits in different organisms. Darwin was quite aware that the morphological differences which systematists use to discriminate between species, subgenera, genera, tribes, families, and other groups often concern surprisingly trivial traits, of no apparent consequence to the organisms involved. It was probably this, more than any other difficulty, which led during the first quarter of the current century to a temporary eclipse of the theory of natural selection. If most differences which we

observe between organisms were adaptively neutral, then it would seem that factors other than selection must be invoked to account for the origin and maintenance of these differences.

It has been repeatedly suggested in biological and anthropological literature, even in recent years, that classification of organisms should be based on adaptively neutral traits. Allegedly, the traits which accurately reflect homology and common descent are neutral, while positively adaptive traits are too easily modified by the environment and are apt to show analogy instead of homology, ecological correspondence rather than common descent. But if so, then the evolution of traits on which the classification is based is a mystery. To use Drosophila again as an illustration: the more than 600 known species of this genus all have three orbital bristles on either side of their heads, and the anterior of these bristles is always proclinate (bent forward), while the other two are reclinate (bent backward). Now, why should this character be retained so tenaciously in so many species? Is it really important for the flies of this genus to have one proclinate and two reclinate orbital bristles?

The basic postulate of the modern biological theory of evolution is that adaptation to the environment is the guiding force of evolutionary change. We need not follow the extremists who insist that all evolutionary changes are adaptive; however, we have to suppose that most organs and functions of most organisms are, or at least were at the time when they were formed, in some way useful to their possessors. Nothing less than this is acceptable if the modern theory of evolution is sustained.

The argument is, then, that our failure to see the adaptive singificance of most traits is simply a measure of our ignorance. Some authors have even urged that assuming neutrality of traits is methodologically inadmissible, since such an assumption allegedly prevents making observations and experiments needed to discover their adaptive significance. The work of several investigators (e. g. Lamotte 1951, 1952) has at the very least shown that supposing some traits to be close to adaptive neutrality may be a fruitful working hypothesis. The usefulness of a trait must be demonstrated, it cannot just be taken for granted. All that can be said is that one's failure to see the adaptive significance of a trait is no proof that it has none. The matter must be settled on the basis of evidence, not by theoretical arguments alone.

It is a fact that the variation in some traits which at one time seemed neutral was later discovered to be adaptive. The chromosomal inversions in Drosophila populations are an example (Dobzhansky 1947); the colors and color patterns of Cepaea snails are another (Cain and Sheppard 1954). But it is still as true today as it was in Darwin's day that the adaptive significance of most traits which vary between and within species is obscure. Suffice it to mention that practically nothing is known about the significance of most traits which vary between races of man as well as among individuals within a race. Although Coon (1955) has made some

interesting suggestions concerning the possible roles of such apparently neutral human traits as the form of the nose, lips, hair, and similar variations, the matter awaits experimental verification. When one considers traits in which species of insects and other organisms often differ, such as the differences between Drosophila species mentioned above, the supposition that all or even most of them are directly useful to their possessors stretches too much one's credulity.

CORRELATION OF TRAITS

At this point we should inevitably inquire whether the impasse which we seem to have reached in our argument may be due to a faulty statement of the problem. A visible "trait" is an outcome of the occurrence of certain developmental, physiological, and ultimately physico-chemical, processes in the organism. Traits, such as the presence of one proclinate and two reclinate orbital bristles in Drosophila, need not by themselves be of any particular importance to the animal. In fact, some Drosophila mutants have one or more of the orbital bristles missing, and the mutant flies seem to suffer no inconvenience on this account. But the processes which result in the formation of certain bristles may give rise also to the other traits, morphological and physiological, in the same organism. The proclinate or reclinate position of a bristle, though quite unimportant in itself, may be an outward visible sign of the occurrence in the organism of quite important developmental processes. The latter are not necessarily disturbed when other factors cause some particular bristle to be missing; a mutant may survive without it. However, if a bristle is formed at a certain point of the hypoderm it is determined either as proclinate or reclinate (Stern 1954). The fixation in the phylogeny of Drosophila of this and of other apparently equally unimportant traits as generic or specific characteristics is, then, a consequence of the adaptiveness of the processes of which these traits are the concomitants.

It cannot be stressed too often that natural selection does not operate with separate "traits." Selection favors genotypes the carriers of which transmit their genes to succeeding generations more efficiently than do the carriers of other genotypes. Now, the reproductive success of a genotype is determined by the totality of the traits and qualities which it produces in a given environment. A disadvantage in some respects may be compensated by advantages in other respects. Thus, in an experiment of the writer with laboratory populations of Drosophila, a genotype which was weaker than another genotype in larval competition under crowding had nevertheless a higher adaptive value, presumably because of a higher fecundity of adults (see also Birch 1955). When a trait is a part of a complex, a system, or a syndrome of developmentally correlated characters, it is obviously the whole system which is favored or discriminated against by natural selection. This is not contradicted by the fact that some one character may be of paramount significance in deciding the success or

failure of a genotype in a given environment and at a given time. Frost resistance may be decisive during hard winters, and drought resistance during dry summers.

PLEIOTROPISM

When genotypes which differ in a single gene yield phenotypes which are unlike each other in two or more not obviously related traits, this gene is said to have pleiotropic, or manifold, effects. Examples of pleiotropism are common. The classical mutants of Drosophila were detected and identified almost always by some externally visible abnormalities in the structures of the adult fly. And yet, these mutants manifest very often also some variations in the viability, fertility, longevity, and/or other physiological characteristics. When such mutants are submitted to the action of natural selection, their fate is likely to be determined not by their obvious externally visible characteristics but by the more subtle physiological ones. Reed and Reed (1950) and Merrell (1953) found that the white-eyed mutant of *Drosophila melanogaster* is discriminated against by natural selection in certain experimental environments; however, this occurs not because their pigmentless eyes make the white flies blind, but chiefly because the females, both red-eyed and white-eyed ones, accept the advances of normal red-eyed males more often than they do those of the white-eyed males.

Quite trivial, and by themselves adaptively neutral traits, may then, be established or eliminated by natural selection because they are components of genetic syndromes which contain also some selectively effective features. It is unimportant in this connection whether the different parts of a syndrome are due to a multiple "primary" action of a gene or to branching of a single "primary" action in the development. This distinction (Grüneberg 1938) has operationally little meaning at the present level of our knowledge. Whether or not genes produce different "primary" products in the same or in different tissues at different stages of the development is an intractable problem which has not been solved. Regardless of what may be its eventual solution, the characteristics of animals or plants which appear striking to our eyes are often less important to their possessors in the struggle for life than the less obvious genetic and developmental correlates of these characteristics. In looking for an explanation of the evolutionary behavior of a trait the adaptive significance of correlated traits cannot be ignored.

The evolutionary importance of pleiotropism is not lessened by the fact that most mutations of single genes are reflected on the phenotypic level by altering some one trait apparently more strongly than others. For example, known mutations at the white locus in Drosophila all affect the eye color, no matter what other characters they may influence at the same time. White is supposed to be an "eye-color gene." In microorganisms, mutations which are characterized biochemically usually affect one and only one step in some reaction chain. But it should not be forgotten as it often is,

that by comparing phenotypic effects of gene alleles A_1 and A_2 we learn at most which developmental processes are influenced by the *difference* between these alleles. We still do not know the total extent of the field of action of either A_1 and A_2. To find this out, it is necessary to compare the effects of the absence (deficiency) of the gene A with those of its presence. But even when this is possible, one cannot be sure that genes homologous to A are not carried in the same genotype at other loci. Recent work on pseudoalleles has indeed shown that gene duplication occurs in the evolutionary process more often than previously known. One cannot exclude the possibility that the presence in the genotype of at least one unit of every kind of gene which a species possesses may be essential for the life of the carriers of this genotype.

GENES AND DEVELOPMENTAL SYSTEMS

Pleiotropism is clearly a part of the story of the establishment in evolution of apparently useless traits, but it can hardly be the whole story. The problem is really insoluble as long as we think of every gene as controlling one or more traits or processes in isolation from the development of the organism as a whole. What, indeed, are the particular adaptively important traits which are correlated with the presence of one proclinate and two reclinate oral bristles in Drosophila? Perhaps such traits will some day be discovered, but at present it may be useful to explore the possibilities of other and more general solutions.

The development of an individual spans the interval of time which begins at fertilization of the ovum and concludes at death. The sequence of events which occur during this time is described most easily in terms of the appearance, persistence, and disappearance of various "traits" and "processes." The same is true of phylogenetic development, except that at least the beginning of the sequence of the events is here always lost in the dimness of the past. For example, we do know, or reasonably infer, that in the human ancestry the trait "erect posture" appeared, and the trait "facial prognathism" disappeared, at a certain time.

In so describing our observations on the ontogeny or the phylogeny one should, however, keep in mind that the individual and phylogenetic developments do not consist of a series of discrete events but are really continua in time. The isolation of "traits" is, then, only a semantic device valid and useful in recording our observations. However, the usefulness and validity of this device lapse as soon as the "traits" begin to be thought of as having independent existence. But this is precisely what all too often happens in the thinking of many biologists. Both the ontogeny and the phylogeny are visualized as building a kind of mosaic picture or as putting together a jigsaw puzzle. The stones of the mosaic, or the pieces of the jigsaw puzzle, are the traits, each determined by one or by several genes, which are gradually assembled by accretion until the picture (organism) is complete, or until it reaches the state in which the observer studies it. Now, this is a shockingly unrealistic way of representing either

the ontogenetic or the phylogenetic development. It becomes a source of pseudo-problems, one of which may be the apparent prevalence of traits which seem to have no adaptive function to perform in the organisms which possess them.

Here we come upon a paradox no biologist should avoid facing. Among the major achievements of modern biology is the discovery that the heredity which is handed down from parents to offspring is a constellation of self-reproducing corpuscles of molecular dimensions, genes. Yet, the development of individuals, as well as the evolution of Mendelian populations, are highly integrated processes. Even if the genes had each a single primary function, such as the production of a single enzyme (which may well be questioned), it would remain true that their effects are woven together on the developmental level into a single system which undergoes orderly changes in time. Genes do not determine each a separate trait; they determine, jointly and severally, the developmental processes which result in the appearance of all the traits which an organism possesses at all stages of its life cycle.

The fact that the changes known at the locus "white" in Drosophila alter the eye color of the fly does not exclude the possibility that this locus has other functions as well. As stated above, the white mutant indeed shows biotically important characteristics which are not obviously related to the color of its eyes. It is even more misleading to say, as is frequently done, that the eye color is formed by the gene white. Although in order for the pigment to be formed and deposited in the eyes the presence of certain alleles of this gene is necessary, many other genes are known which also influence the formation of the pigment and the development of the eyes. Microcephalic idiocy in man may be due to a mutation in a certain gene, but it does not follow that the human head is formed by that gene. Formation of the head is an outcome of embryonic and post-embryonic development which is influenced by probably all the genes which the organism has, and the presence of most and perhaps of all these genes is indispensable for the development to proceed normally. The genes are to some extent independent of each other in the processes of the transmission of heredity from parents to offspring, even though studies on position effects and on partial allelism suggest that this independence is not as complete as classical geneticists liked to think. By contrast, the processes of development cannot be divided in autonomous components governed by single genes. The verbalisms borrowed from studies on the transmission of heredity are often misleading when applied to the phenomena of development. It is unfortunate that this illegitimate transfer of words, and of habits of thought which go with them, is nevertheless a common practice with geneticists.

On the population level the genes are rarely autonomous. Genes as such are subject to natural selection perhaps only in simplest viruses. Elsewhere it is not a separate gene but the genotype of which it is a part that

is favored or discriminated against by selection. Moreover, the adaptive value of the genotype is manifested in the fitness of the phenotypes which it engenders in its carriers when the latter develop in certain environments. It is not the genotype but a living individual who exhibits a certain succession of phenotypes at different stages of its life, and who survives or dies and succeeds or fails to reproduce. And, as pointed out above, the success or failure are decided by the competence of the phenotype not merely in the adult but at all stages of the life cycle. No matter how healthy may be an infant or a larva or a seedling, the Darwinian fitness of the organism is zero if the adult is inviable or sterile. Conversely, high infant mortality is a drawback even if the survivors are vigorous as adults.

ADAPTEDNESS AND THE DEVELOPMENT PATTERN

The phenotype of an individual may be said to follow a certain trajectory in time; this trajectory is determined by the interactions of the genotype with the succession of the environments encountered in the process of living. At any given point on the trajectory the phenotype is decided by its preceding state and by the existing environment. For example, the phenotype of a person at a given moment is the outcome of transformations of his past phenotypes and the base of the future ones. The succession of the changes in a person's phenotype is determined, of course, by the development pattern induced by his genotype and by the successive conditions of the environment.

Let us now consider not the phenotype as a whole but a trait, such as the weight or the state of health or the disposition of a person. Obviously, my weight, health, and disposition are at this moment what they were a moment or several moments ago, except as changed by the ageing process, by diet, weather, occupations, contacts with other persons, etc. I have not inherited any particular "weight," since my weight has varied greatly during the embryonic and post-embryonic life. What I have inherited is a genotype which determines, jointly with the succession of the environments, the trajectory which my weight has followed thus far, and will follow during the remainder of my life.

Sheldon (1954) has attempted to trace the trajectories of weights at different ages and for different body heights for all his somatotypes. These trajectories apply, as acknowledged by Sheldon himself, to development patterns only in environments which are regarded as normal or standard. In other environments the weights may be either higher or lower, and it is gratuitous to regard any weight as inherent or intrinsic for a given somatotype or genotype. All weights which a person may have in any environment, normal or abnormal, salubrious or morbid, are equally inherent and fixed by the norm of reaction of a given genotype to a given succession of environments. This in no way reduces the importance of knowing just what weights individuals of a given somatotype will develop under different circumstances, since different people show different development patterns

in environments which are very nearly similar. The same holds for intelligence or for any other trait. There is no such thing as "intrinsic intelligence," unless this is arbitrarily defined as that evolved in a certain environment; neither is there any known upper or lower limits of intelligence, unless certain environments are considered to be the only possible ones. All this does not mean that intelligence is not conditioned genetically; it is, for each set of environments. It would be invaluable to know how persons of different genotypes would develop in different environments, and knowing this should be the aim of experiments with different educational systems.

Although no phenotypic trait is any more "intrinsic" than any other, certain phenotypes exhibit a fitness superior to that of others in the range of the environments in which the species normally lives. The superior developmental patterns and superior phenotypic trajectories are promoted by natural selection, while the inferior ones fail to be perpetuated. Therefore, certain developmental patterns become established in a majority of individuals of every species or population as its adaptive norm. Genotypically conditioned deviations from this norm are hereditary diseases and malformations. Some of them may be "cured," that is, forced back to the normal development trajectory by special environments which are not required by the genotypes which constitute the adaptive norm. Others are incurable, inasmuch as no environments capable of returning them to normal phenotypic trajectories are known.

The fact of crucial importance is that the development patterns which result in adaptively competent phenotypes are homeostatic. They are protected by being buffered against the disruptive effects of environmental changes which are commonly met with in the habitats in which the species normally occurs (Lerner 1954, Dobzhansky and Wallace 1954, Dobzhansky and Levene 1956, Lewontin 1956, and others). Rare or abnormal genotypes, such as homozygotes in a normally outbred species, are often deficient in homeostatic buffering. Nor is homeostasis necessarily shown when normal genotypes are exposed to environments which are unusual for the species. As pointed out especially by Schmalhausen (1949), unusual environments often provoke harmful morphoses instead of adaptive modifications. A nonhereditary disease is, then, a deviant phenotype resulting from the exposure of a normal genotype to an abnormal environment, or a phenotype brought about by senescence which results in a gradual loss of homeostatic adjustments.

A qualification which must be made at this point is that the adaptive norm need not be monolithic; on the contrary, many species and populations are polymorphic, with two or more phenotypic norms which may possess superior fitnesses in different ecological niches. Such polymorphic populations show, then, two or more homeostatically buffered developmental patterns; the development is turned to one of the alternative trajectories by "switch genes" with clear-cut phenotypic effects, or by environmental

stimuli (Mather 1953 and others). But whether monomorphic or polymorphic, the developmental patterns which confer high Darwinian fitness upon their possessors are hedged against environmental disturbances which are met in the usual habitats of the species.

CONCLUSIONS

The notorious difficulty of discovering the adaptive significance of traits in which races and species of animals and plants commonly differ is due in part to an incorrect statement of the problem. "Traits" have no adaptive significance in isolation from the whole development pattern of the organism which exhibits them at certain stages of its life cycle. The phenotype of the individual changes relentlessly from conception to maturity and to death; the path which these changes follow is set by the genotype interacting with the succession of the environments to which an individual is exposed. A "trait" may, then, be defined as an aspect of all or of a certain portion of the path or the trajectory of the development. However, it is the trajectory as a whole which confers upon the genotype or the individual its fitness to survive and to reproduce.

When the phenotypic manifestations of two or more genotypes are compared, it may appear that they differ in adaptive values because of some few aspects, or traits, of their development patterns. Yet we must beware of thinking of a development pattern as though it were a sum of independently variable traits. When we wonder why a proclinate oral bristle has not become reclinate, or vice versa, in some species of Drosophila, we implicitly assume that the position of a bristle is decided by a genetic factor or a developmental event which is inserted among other factors and events, but which is not a part of any organized pattern of interrelated processes. Such an assumption is more likely to be wrong than right.

The same assumption is implicit when it is asked why some vestigial organs of the human body have not disappeared completely, as some of them have done in other species, or vice versa. We still possess traces of the muscles that in other mammals move the ears, still harbor the coccyx, an utterly useless relic of the ancestral tail, and some of us are troubled by the vermiform appendix of the coecum, an organ which, for example, the cats have disposed of entirely. Mammalian embryos are full of organs which are formed seemingly only to disappear without ever functioning; the gill bars and the notochord seem to be used only as treasured examples of the biogenetic law and as "proofs" of the occurrence of evolution. However, a complete disappearance of these useless organs, both in the adults and in the embryos, would necessitate radical changes in the basic embryonic processes of organ formation and differentiation. The coccyx is a part of the axial skeleton, and the gill bars arise in the process of formation of the head and the neck. The problem should, therefore, be turned around, and it may be asked what advantages would accrue to the organism from such radical alterations of its development. The development is more than

summation of "unit characters" or unit processes. As emphasized especially by Schmalhausen (1949), development is a highly integrated process, and progressive evolution from the lower to higher organisms has on the whole tended to make the integration more and more thorough, and to make the basic developmental processes more and more autonomous from direct stimuli emanating from the environment.

SUMMARY

A trait is an aspect of the whole or of a certain portion of the developmental pattern of the organism. An adaptive trait is, then, an aspect of the developmental pattern which facilitates the survival and/or reproduction of its carrier in a certain succession of environments.

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A COMPARATIVE STUDY OF ANTS IN DESERT REGIONS OF CENTRAL ASIA AND OF SOUTH AMERICA

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INTRODUCTION

The basic postulate of the modern theory of evolution is that the environment furnishes the challenges to which living organisms may respond by adaptive transformations of their structures and functions, these transformations mediated by the processes of mutation, sexual recombination, and natural selection. It follows, then, that similar environmental conditions should furnish similar challenges, and might provoke similar responses. Similar physical environments occur in different parts of the world, often separated by extensive territories in which quite different conditions are prevalent. Thus, the desert belts of the Northern Hemisphere of the Old World (Sahara, Arabia, Iran, Turkestan, Mongolia), and of the New World (western North America) are separated by oceans or by tropical forests and savannas from each other and from the deserts of the Southern Hemisphere in South America, southern Africa, and Australia. It is well known that analogous forms of life, such as, for example, xerophytic plants with fleshy stems and reduced leaves, have evolved in different deserts and often from quite unrelated plant families, such as among Cactaceae in America and Euphorbiaceae in Africa. Nevertheless, it would be an exaggeration to say that similar environments always evoke similar responses in the organisms which inhabit them, and these lacks of parallelisms are perhaps just as interesting for our understanding of the evolutionary mechanisms as are the instances of parallel developments.

The present article compares the ants which inhabit the desert regions of Asia, particularly Turkestan, and of South America, particularly Argentine. It is based on personal observations of the author (Turkestan 1922/1934, Argentine and Bolivia 1947-1955). The desert regions compared are separated widely by seas and by continents with more humid climates. The desert regions merge into adjacent more humid zones; the Argentine desert is adjacent on the north to the tropical part of South America, and on the west to the humid southern Chile; the deserts of Turkestan are bounded by the mountains to the east and to the south, and by the steppes of southern Siberia to the north. The existence of more or less wide intermediate zones facilitates the evolutionary connections between the deserts and the adjacent non-desert zones.

TURKESTAN AND ARGENTINE DESERTS COMPARED

The outstanding similarities between the zones compared are due, of course, to their aridity. Otherwise they differ in a number of respects. (A)

Turkestan is an eastern extension of the Mediterranean region lying approximately between the latitudes 37° and 40° N. The principal constituents of the ant fauna are more or less the same throughout, from Turkestan to northern Africa. The ant fauna of Tashkent resembles that of Iraq (Weber 1952). The desert region of Argentina is elongated meridionally, from the Strait of Magellan to the Tropic of Capricorn, and farther northwards to the high plateau of Bolivia and the Pacific Coasts of Chile and Peru. (B) The deserts of Turkestan are chiefly low plains, and at elevations higher than 500m in the adjacent mountains there appear mesophilic elements. Argentine deserts start at the sea level in Patagonia, but reach elevations of 5000m and higher in the North. The fauna of the Altiplano of Bolivia resembles that of Mendoza and of Patagonia. Some ants (*Camponotus Bruchi* Forel) occur as high as 4500m a.s.l. By contrast, the ant fauna of high Tibet is very different from that of Turkestan; the former has an only slight admixture of mediterranean elements, and is essentially that of the boreal type (the genera Myrmica, Formica, etc). (C) The deserts of Turkestan are isolated from the humid tropical zones, while those of Argentine merge into more humid regions, to the tropical forest inclusive. (D) The deserts of Turkestan are humid and cold in winter (the absolute minimum temperature in Tashkent is −29.5°C); those of Argentina are dry but less cold in winter, and have rains chiefly during the summers (the absolute minimum for Mendoza, elevation 768m, registered between 1928 and 1937 is −8.0°C). The overwintering conditions for the ants are evidently different.

Because of the above differences, one may expect that the ant faunas of the deserts in question would be derived from philogenetically different sources, but should show some parallelisms because of adaptation to similar habitats.

THE CLASSIFICATION OF ANTS

As a basis for the discussion to follow, a brief review of the nine subfamilies into which the family of ants (Formicidae) is divided must be given here.

A. *Relatively primitive subfamilies.* Workers and females with a well developed sting. Females more or less resemble workers; the latter are monomorphic. Larvae are active, and are able to feed independently. The colonies are small. Cooperation between the workers from the same colony little developed.

1. Ponerinae. Mainly termophilic or mesophilic. Absent in the desert of Central Asia, in Argentina represented by a single species, *Ectatomma quadridens,* relatively little adapted to desert habitats.

2. Cerapachyinae. A rather small termophilic or mesophilic group. Not represented in deserts, at least in both areas compared.

3. Myrmeciinae. One of the primitive subfamilies, which occurs in a variety of environments only in Australia (bulldog ants, sergeant ants).

TABLE 1

SYSTEMATIC POSITION OF THE ANTS WHICH INHABIT DESERTS OF CENTRAL ASIA AND OF ARGENTINE

Subfamily	Genus	Central Asia	Argentine	Eastern Patagonia
Ponerinae	Ectatomma	–	+	–
Dorylinae	Eciton	–	+	+
Pseudomyrmecinae	Pseudomyrmex	–	+	–
Myrmicinae	Pogonomyrmex	–	+	+
	Elasmopheidole	–	+	+
	Pheidole	+	+	+
	Messor	+	–	–
	Monomorium	+	–	–
	Solenopsis	–	+	+
	Oedaleocerus	–	+	–
	Crematogaster	+	+	–
	Cardiocondyla	+	–	–
	Tetramorium	+	–	–
	Wasmannia	–	+	–
	Atta	–	+	–
	Acromyrmex	–	+	+
	Mycetophylax	–	+	+
Dolichoderinae	Tapinoma	+	–	–
	Araucomyrmex	–	+	+
	Conomyrma	–	+	+
	Dorymyrmex	–	+	+
	Forelius	–	+	+
Formicinae	Brachymyrmex	–	+	+
	Plagiolepis	+	–	–
	Acantholepis	+	–	–
	Proformica	+	–	–
	Cataglyphis	+	–	–
	Formica	+	–	–
	Camponotus	+	+	+

TABLE 2

NUMBERS OF GENERA BELONGING TO VARIOUS SUBFAMILIES IN THE DESERTS OF CENTRAL ASIA AND OF ARGENTINE

Subfamily	Turkestan	Argentine
Ponerinae	–	1
Dorylinae	–	1
Pseudomyrmecinae	–	1
Myrmicinae	6	10
Dolichoderinae	1	4
Formicinae	6	2
Total	13	19

B. *Adult ants morphologically primitive, larvae specialized and are fed by the workers.*

4. *Pseudomyrmicinae.* Mostly wood ants, absent in Central Asia. In Argentine two species are known: *Pseudomyrmex gracilis* (living in wood) and *Ps. denticollis* (in the soil). Both species related to forms living in the tropical zone to the north.

C. *Phylogenetically more advanced groups.*

5. *Leptanillinae.* A small group related to the following.

6. *Dorylinae.* Nomadic predators forming very large colonies, but usually having no permanent nests (there are, however, some exceptions). Widespread in the tropics both of the Old and of the New World. Not represented in the deserts of Central Asia; in the deserts of India, western Asia, and Africa represented by the genus Dorylus; in the Argentine deserts represented by the genus Eciton, the species of which have close relatives in the tropics of South America.

D. *Most highly evolved groups.* The cooperation between the workers of a colony is highly developed. Showing a tendency towards a plasticity of behavior at different ages, contrasting with the gregariousness of the preceding subfamily. Larvae are fed by the workers. Often showing complex biosocial relationships between different species and genera (slave makers, social parasites).

7. *Myrmicinae.* Workers and females with a sting which may be well developed or more or less strongly reduced (Attini). This subfamily occurs in humid as well as dry, hot as well as cold countries; abundantly represented in South America.

8. *Dolichoderinae.* The sting is absent in both females and workers. This subfamily seems to have been dominant during Tertiary times (Baltic amber, Florissant), now abundant only in Southern Hemisphere and very common in deserts of Argentina.

9. *Formicinae.* Females and workers without a sting. The dominant subfamily at present, most developed in the Northern Hemisphere and in the tropics of the Old World, less so in South America.

SPECIALIZED ECOLOGICAL TYPES OF DESERT ANTS

1. *Hunting ants.* Ants which catch their prey running on the surface of the soil. They develop considerable speeds in sunny weather and at high temperatures. The hunters are working singly, not forming groups of columns of individuals. This ecological type is characterized by an elongation of the thorax and of the legs as well as by a well developed psammophore. Moreover, they frequently have adaptations which permit them to avoid excessive heating of the body tissues even with intense activity during the noon hours. Among these adaptations the most conspicuous ones are pale body colors, dense silvery pilosity, and, in some species of Cataglyphis, reducing the surface of the integument facing the sun by holding the abdomen vertically upwards. It may be noted that these adaptations tend to be alter-

natives: the forms which have the habit of holding the abdomen vertically usually lack the pale colors and the silvery pilosity.

2. *Granivorous ants.* This ecological type, at its most highly specialized level, is characterized by the following traits. (A) The workers have more or less massive bodies with relatively short but powerful legs; the locomotion tends to be slow. (B) The chief or sole source of food are seeds. (D) The seeds are transported to the nest over trails which radiate from the nest's entrance. (E) Inside the nest the seeds are cleaned of glumes and other protective covers, and the covers are removed from the nest forming accumulations near the entrance. (F) The seeds are stored in subterranean chambers, and the ants prevent their germination; the occasional seeds which do germinate are thrown out of the nest. (G) The ants work in organized groups, forming columns of workers who transport the seeds to the nest. (H) These columns may be very large, numbering thousands of individuals. In less specialized representatives of this ecological type some of these traits may be absent.

3. *Ants which cultivate fungi.* The most highly specialized forms of this type (the genus Atta) possess the following traits. (A) Colonies are large, consisting of thousands of individuals. (B) Nests are subterranean, with numerous fungus "gardens," each in a separate chamber. (C) The nests have a system of subterranean galleries serving different functions, such as transportation of the leaves, extraction of the used-up mycelium, ventilation, etc. (D) Subterranean chambers for refuse (used-up mycelium, remains of the dead ants, etc). (E) The nests have many openings, from which radiate trails over which move the workers procuring leaves on which the fungi are to be grown. (F) A division of labor among morphologically differentiated workers; small workers cultivate the mycelium and take care of the larvae, larger ones collect leaves and transport them to the nest, the largest of all are "soldiers" which defend the nest from intruders. (G) The workers work in groups the members of which cooperate with one another.

In the more primitive representatives of the same ecological type the workers are uniform, the colonies are small, and use feces of caterpillars and other insects as the substrate for the cultivation of fungi.

HUNTING ANTS IN THE DESERT OF CENTRAL ASIA AND OF ARGENTINA

As an ecological type, a hunting ant seems to be a simpler adaptive system than a granivorous, and especially a fungus-growing form. Hunting ants occur even among the primitive subfamily Ponerinae, although they do not reach high levels of specialization. *Ectatomma quadridens* is a hunter belonging to the above subfamily, which occurs in the Argentine desert. This species does not, however, penetrate the most arid parts of the desert, being confined to the marginal northeastern zone. It interrupts its activity during the hottest hours of the day, and lacks the adaptations which prevent the overheating of the body. Species related to it are mesophilic.

More highly specialized hunting ants have evolved both in the deserts of Argentine and in those of Central Asia. But while in the former region they belong to the subfamily Dolichoderinae, in the latter region they have developed in the subfamily Formicinae. This is a splendid example of a convergent development of similar ecological types in quite different phyletic lines.

In Central Asia the hunting ants belong to a single genus, Cataglyphis, which does not occur in the New World at all. This genus is a member of a group of rather closely related forms the relationships between which may be represented as in figure 1.

This entire group of forms belongs to the Old World, has some representatives in the temperate and cold areas of North America, and is quite foreign to South America. The morphological differences between Proformica and the less highly specialized Cataglyphis amount chiefly to a change in the body proportions towards elongation of the body and of the extremities (in Cataglyphis). *Cataglyphis cursor* lacks the adaptations characteristic of the desert hunting ants: its coloration is dark, the abdomen is held horizontally, no silvery pilosity. It lives only at the periphery of the arid zone and in mountains. *C. pallidus* already has a pale color, matching that of sand, and it lives only in sandy deserts. Among the more specialized Cataglyphis, *C. albicans* and *C. bicolor* hold the abdomen vertically upwards. Both species are common in the deserts of Central Asia. *C. bombycinus* shows a dense silvery pilosity, and the rapidity of its movements reaches the upper limit among ants. It lives in the deserts of Africa.

The hunting ants of Argentine deserts belong to the genus Dorymyrmex. The phylogenetic relationships of this genus can be represented as follows:

Iridomyrmex
↓
Araucomyrmex
↓
Dorymyrmex

Iridomyrmex is a pantropical genus, well represented in the Baltic amber, and at present most highly differentiated in Australia, where some desert-dwelling species are known. It is represented in Argentine by the mesophilic *I. humilis*, which has been introduced and became a pest in Mediterranean countries, in Hawaii, and in other places. Araucomyrmex is a close relative of Iridomyrmex, living in Chile, Patagonia, and in the Andes till about the 30° latitude South. It lives, consequently, only in zones adjacents to the deserts having more or less temperate climates.

Dorymyrmex is a derivative of Araucomyrmex adapted to live in deserts. Its species occur in the Argentine deserts, in the Bolivian and Paraguayan Chaco, and in drier upland valleys of Bolivia, up to 3000m elevation (near Cochabamba). It is not found in Chile. The North American species which are sometimes placed in the genus Dorymyrmex actually belong to a different genus, Conomyrma.

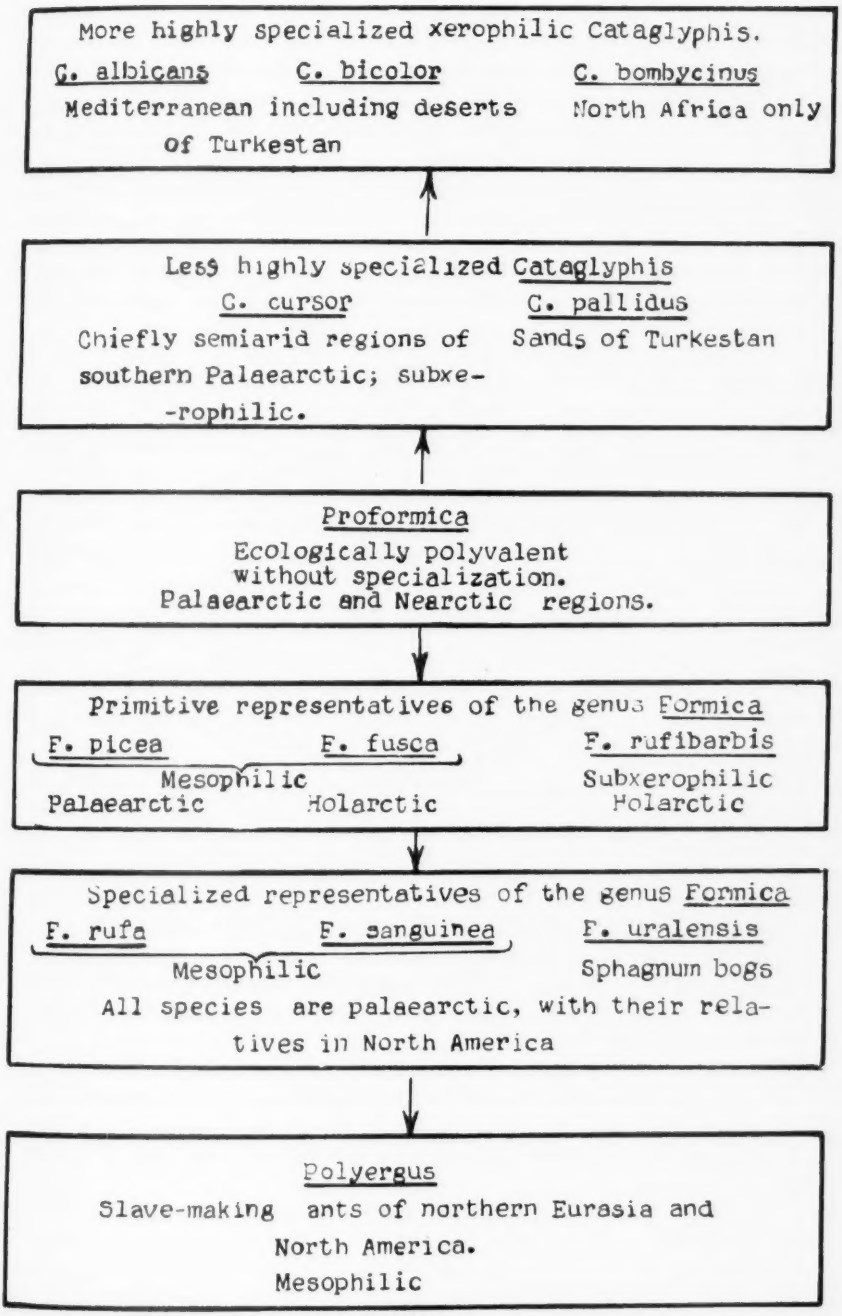
More highly specialized xerophilic Cataglyphis.
C. albicans
Mediterranean including deserts of Turkestan
C. bicolor
C. bombycinus
North Africa only
Less highly specialized Cataglyphis
C. cursor
Chiefly semiarid regions of southern Palaearctic; subxe--rophilic.
C. pallidus
Sands of Turkestan
Proformica
Ecologically polyvalent without specialization.
Palaearctic and Nearctic regions.
Primitive representatives of the genus Formica
F. picea
Palaearctic
F. fusca
Holarctic
Mesophilic
F. rufibarbis
Subxerophilic
Holarctic
Specialized representatives of the genus Formica
F. rufa
F. sanguinea
Mesophilic
F. uralensis
Sphagnum bogs
All species are palaearctic, with their relatives in North America
Polyergus
Slave-making ants of northern Eurasia and North America.
Mesophilic

FIGURE I.

The point which is most important for our purposes is that in the evolution of Dorymyrmex one finds the same adaptive trends which we have seen in the systematically as well as geographically remote Cataglyphis. These tendencies are: elongation of the body and the extremities, pale coloration, and reduction of the body surface exposed to the sun. Interestingly enough, the development of these adaptive traits has failed to reach in any species of Dorymyrmex the high levels which it has reached in Cataglyphis. Roughly speaking, the most highly advanced Dorymyrmex have not exceeded the level of desert adaptation found in the relatively unspecialized *C. pallidus* (see above). Species of Dorymyrmex are not very rapid runners, and their activity usually becomes somewhat depressed during the hottest hours of the day.

GRANIVOROUS ANTS IN THE DESERTS OF CENTRAL ASIA AND OF ARGENTINA

Granivorous ants have developed in the arid zones all over the world, but, interestingly enough, they have developed from different phylogenetic sources in different regions, although they all belong to the same subfamily, Myrmicinae. In the deserts of Central Asia this ecological type is represented by the genus Messor, the species of which possess in highly developed form all the specialized traits of the granivorous type enumerated above. *M. barbatus* is the dominant ant species not only in Turkestan but also in deserts of western Asia and of northern Africa; this is the ant which attracted the attention of the ancients and deserved a mention in the writings of King Solomon.

In the Argentine deserts the situation is quite different. At least four different genera have "attempted" to solve the "problem" of evolving a granivorous ecological type, yet not one of them succeeded in reaching the level of specialization found in the genus Messor of the Mediterranean region. The nearest approach to Messor is found in the genus Pogonomyrmex, which contains some fairly large, massive bodied ants with short but strong extremities. The workers of Pogonomyrmex are monomorphic or with only slight polymorphism (*P. coarctatus*). The morphological parallelism between Messor and Pogonomyrmex is emphasized by the presence of the so-called psammophore. The Argentine species do not build trails for the transport of seeds, and do not make large stores of seeds in the subterranean chambers of their nests.

The genus Pogonomyrmex is exclusively American, having two disjunct distribution areas, one in the Argentine and the other in the United States, in both countries living chiefly in arid territories (Kusnezov 1951). This genus is known in fossil condition (Florissant beds, Carpenter 1930), and its high taxonomic differentiation in the Argentine suggests that it is geologically ancient. Its failure to evolve highly developed granivorous specializations cannot, therefore, be explained either by its youth or by a young geological age of the deserts of Argentine (Kusnezov 1951).

The phyletic roots of the genus Pogonomyrmex are to be looked for apparently in the American tropics, where are found living at present the mesophilic relatives Hylomyrma, Forelomyrmex, etc. This inference is supported by the distribution of the genus Ephebomyrmex, which represents a branch of a phyletic trunk common with Pogonomyrmex. Ephebomyrmex has several species in tropical and subtropical parts of South America, Central America, and in Southern United States; species endemic to the Antilles; and a group of 3 peculiar species in the humid western Patagonia and southern Chile. The distribution area of this genus is, then, discontinuous; its species do not occur in arid zones, or if they do are rare there. The "conquest of the desert" by the originally mesophilic forms seems to be clear enough, though the details of this process need more study.

The other three genera which evolved granivorous forms in the Argentine are Elasmopheidole, Pheidole, and Solenopsis. They have small workers and large soldiers with particularly large heads. In every case, the desert granivorous species are clearly related to unspecialized mesophilic ones. Another fact worthy of note is that, in Elasmopheidole and in Pheidole, the degree of the development of the granivorous specialization is positively correlated with a progressive increase in the sizes of the workers and soldiers. Thus, *Elasmopheidole aberrans* and *Pheidole spininodis* live in the most arid regions, sometimes are the dominant ant species in such regions, and are the largest representatives of the respective groups. The increase in size may conceivably be related to the greater complexity and the greater depth of the subterranean nests which are needed in the deserts.

FUNGUS-GROWING ANTS ARE CONFINED TO THE NEW WORLD

This ecological type of ants occurs exclusively in the New World, and is lacking in the Old. The fungus-growers belong to the tribe Attini of the subfamily Myrmicinae (see above). The lack of Attini in the Old World can hardly be accounted for by supposing that they have become extinct there. This tribe is unknown in fossilized condition; moreover in the New World, Attini live in all sorts of geographic environments, and some of its species are among the ecological dominants of the neotropic fauna.

In the Argentine deserts the highly specialized fungus growers are represented by two species of Acromyrmex (*A. lobicornis* and *A. striatus*), and one species of Atta, the precise taxonomic status of which is still unclear. All three species are very common. Nevertheless, they have close mesophilic relatives in the tropical zone. There is no doubt that the "conquest of the desert" has been accomplished by originally mesophilic forms.

Some less highly specialized fungus growers have also succeeded in occupying desert habitats. In the provinces of Mendoza and La Rioja, as well as in other parts of the arid zone, there are commonly found species of the genus Mycetophylax. The nests of these ants are small, with usually a single chamber containing a fungus "garden," but this chamber is located at a considerable depth under the surface of the soil (up to 1½ m and more). The ants are active not only in summer but also in very dry winter. My-

cetophylax is, however, the only one among the primitive genera of Attini which succeeded in populating the arid zone, in which it is even more abundant than in the more humid regions. One may conjecture that Mycetophylax is a more ancient migrant from the mesophilic tropical zone into the arid regions than are the more specialized fungus growers. In this connection, it is interesting that fungus-growing ants are absent in Chile. This may indicate that this ecological type is phylogenetically young, and that its absence in Chile may be accounted for by the isolation due to the uplift of the hight range of the Andes. In Bolivia, *Acromyrmex seriatus*, a representative of Attini, lives however at elevations of 3500m and higher. Its existence there may be favored by the intense insulation of the soil during the winter months, which permits uninterrupted growth of the fungus gardens.

It is, then, clear that: (A) Fungus-growing ants represent a highly specialized and statistically improbable form of life. (B) This form of life has been highly successful in the New World, under mesophilic as well as under desert conditions. (C) This form of life has evolved only in the New World, and has no parallels at all in the Old World. Identical, or at any rate similar, challenges have evoked an evolutionary response in this case only in American ants, and no response in the Old World. Clearly, then, an environmental challenge by itself does not guarantee the occurence of uniform response in different places and at different times.

OTHER DIFFERENCES BETWEEN THE ANT FAUNAS OF CENTRAL ASIA AND OF ARGENTINA

Arboricolous ants are absent in Central Asia, and common in the Argentine. An example is *Pseudomyrmex gracilis*, which lives in the tropical South America as well as in the Argentine deserts. Its distribution extends southwards to the province La Rioja, but it is absent in Chile. The arboricolous habit places the ant in a microenvironment which is suitable for essentially mesophilic forms. Arboricolous ants are very common in western Chaco, despite its long and very dry winters.

Deserts of Central Asia lack gregarious nomadic ants of the subfamily Dorylinae, which are not uncommon in the subtropical deserts of northern Argentine and which go southwards to the provinces of Mendoza and Rio Negro.

These differences between the Asiatic and the South-American deserts may be related to the fact that the arid zone of the Argentine merges gradually into the humid tropical zone farther northwards. This facilitates the passage and adaptation of mesophilic forms to the arid zone. Central Asia is, on the contrary, isolated from tropical countries by high mountains. It is, nevertheless, impossible to account for all the differences between the ant faunas of the Asiatic anc South-American deserts on this basis.

One of the important constituents of the Mesophilic fauna of western Patagonia and of southern Chile is the primitive subgenus Notomyrmex of

the genus Monomorium. Now, Monomorium has a wide distribution, extending in the Southern Hemisphere to Australia and to New Zealand. It is evidently a very ancient group which has lived for a long time in the southern part of South America. And yet, Monomorium has evolved desert-dwelling forms in Australia, Africa, the Mediterranean Region, Central Asia, but not in South America.

Thus, neither environmental challenges, nor the availability of similar ancestral forms, nor both, are sufficient to guarantee the appearance of similar ecological types adapted to living in deserts. We are forced to visualize evolution as a natural creative process, in which the potentialities of organic forms may or may not be realized through the mechanism of natural selection. Ecologically parallel forms of life may arise from phylogenetically different and sometimes not even closely related sources. A conception of the creative nature of evolution similar to that presented in this paper on the basis of studies of systematics and ecology of ants has recently been developed on a genetic basis by Dobzhansky (1954, 1955).

SUMMARY

1. The ant faunas of the deserts of Central Asia and of Argentina are phylogenetically different in origins, and are related to the faunas of the neighboring non-desert regions.

2. The desert faunas show remarkable parallelisms, due to the presence of similar ecologically specialized types, such as hunting ants and granivorous ants. At the same time, other ecological types are conspicuously absent in one or the other fauna. Thus, fungus-growing ants are absent in the Old World, while the hunting and the granivorous ants have reached higher levels of specialization in the Old than in the New World.

3. These differences and lacks of parallelisms cannot be accounted for either by different geological ages of the deserts compared, or by the presence or absence of suitable ancestral types of ants which could produce forms adapted to desert living. Thus, the genus Monomorium has given rise to desert dwellers in the Old World, but not in deserts of South America.

4. Similar environmental challenges do not, therefore, produce necessarily similar evolutionary responses of the living matter. Evolution is a natural creative process. Phyletically different organic materials may, because of the action of natural selection, yield parallel ecological types. These ecological types become then components of functional systems, which are the faunal complexes of deserts and of other types of habitats in different parts of the world.

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AXIAL ROTATION AND THE ORIGIN OF VERTEBRATES

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The origin of the vertebrates from their hypothetical invertebrate ancestors has never been fully explained. The many theories that have been put forward betoken their inadequacy by their very multitude. Almost every phylum of the invertebrate stock has in its turn been laid under charge as the common ancestor. The present trend of biological opinion turns on embryological evidence, in which, in the opinion of some, undue attention is paid to the minutiae of extremely simple forms. It is not every biologist who agrees with the weighty conclusions that rely on such microscopic detail for their principal if not only evidence. The major features of vertebrate morphology are left untouched by these embryological theories. Chief of these, and probably the most outstanding in relative importance, is the overall pattern of the nervous system.

There is a complete unconformity between the structure of the nervous system in the higher invertebrates and the lowest vertebrate, the lamprey. The invertebrate nerve-cords are ventral, below the gut, but in the vertebrates the gut or venter is below the nerve-cord. Modern biology has rejected the simplest and most attractive interpretation of this anomaly, which is that vertebrates are merely invertebrates walking on their backs (St. Hilaire, 1822), thus bringing the ventrally placed nerve-cord of the worm and the lobster into the dorsal position it occupies in fishes and man. Dohrn's, (1875) "turn over" theory, however, is far from dead, and there are reasons for believing that Axial Rotation may account for much that is otherwise hard to explain; such for instance as the dorsal pituitary of insects, the rivalry between epithalamus and hypothalamus for the leadership of the cross-brain, and above all the presence and structure of the optic chiasma and the decussating systems of contralateral control to which it has given rise.

THE OPTIC CHIASMA

In the invertebrates, the eye or eyes on the one side of the head are in touch with the cerebral ganglion of the same side: there is no crossing over, as with the vertebrates. The cuttlefish, for instance, has an eye so well patterned that it lacks practically nothing, as regards its optical and physiological essentials, of the structure of the vertebrate eye; only the brain behind it is wanting. There is merely a pea-size optic ganglion attached to each eye and connected by its optic stalk with the cerebral ganglion of its own side. This is the highest development of the invertebrate eye.

In vertebrates, however, the eye on the right-hand side of the head (or that part of it, in mammals, which views the right half of the field) is joined to the left-hand side of the brain. This cross-over or decussation of the optic nerves takes place in the midline chiasma. This discontinuity between uncrossed and crossed control, in the transition from invertebrate to vertebrate, is thus as remarkable as that between ventral and dorsal nerve-cords. It is a matter of some concern, therefore, to seek out the evidence afforded by intermediate stages.

The lancelet, having no head and no cranial eyes, has no chiasma. From its invertebrate forebears it has inherited the mathematical regularity of its longitudinal sigmentation. The lop-sided symmetry of some of its near relatives, however, suggests that these transitional forms have not yet fully adapted themselves to the results of axial rotation.

In fishes, the chiasma is of simple type. The two optic nerves cross over without any intermingling or true decussation of their fibres, like the blades of a pair of scissors. Like scissors, therefore, there are two cheiralities or handednesses, enantiomorphic forms which cannot commute except in a mirror. The two forms (right nerve on top, and left nerve on top) occur in almost exactly equal proportions. Parker examined a hundred specimens each of ten common species of symmetrical fish. "In six of the ten fishes examined the left nerve was dorsal about as frequently as the right, the greatest difference being never more than ten per cent. In the remaining four this difference does not exceed in any instance twenty per cent.... In a total of one thousand the right nerve was dorsal in 514 times, the left 486" (Parker 1903). There was no correlation between the dimorphism of the optic chiasma and the other great dimorphism, that of male and female.

This crossing over of the optic nerves could be accounted for by the two eyes maintaining the same position relative to the outside world as they possess among the invertebrates, while the central nervous axis rotated half a turn along with the rest of the body. This rotation presumably took place indiscriminately to right or left in equal proportion, thus explaining the 50-50 ratio discovered in fishes. The cheirality is probably inherited genetically, as it is known to be among many phyla of invertebrates.

The flat-fishes such as the soles and flounders, for reasons unknown, seem to have rebelled against the ancestral pattern of upside-down living, and have attempted to revert to the status antiquior. A flounder starts life as a symmetrical embryo little different in structure from that of a normally shaped fish. With almost catastrophic suddenness, however, it axially rotates through a right-angle and comes to swim on its side. The under eye, with its visual field cut off, rapidly travels round or through the top of the skull to join its luckier fellow on the upper side, trailing after it the optic nerve (Williams, 1902).

If the axial turn from upright to flat is in the same direction as the previous rotation (of two right angles) that brought the optic chiasma into being, the two optic nerves will be given an extra twist and will be interlaced by a

third and additional right-angle. If, on the other hand, the ontogenetic rotation is in the reverse sense to the phylogenetic rotation, the optic chiasma will be unwrapped to the extent of one right-angle. In the American flounder, the latter condition is invariably the case, and no specimens are recorded in which the chiasma is further complicated by the rotation. It might be thought that this is due to a process of selective mortality which eliminates all the embryos that have rotated in the "wrong" direction; this, however, is not the case, for the cheirality of the flounder is predetermined in its unhatched embryo, all of whom are of the same monomorphic pattern (Parker, 1903).

There is some evidence that this crossing over of the optic nerve is biologically a disadvantage. Certain species of flat-fish exhibit both dextral and sinistral forms, that is they rotate so that the right or the left side comes to lie uppermost. Rarely, a left-handed halibut is found; the Californian halibut and the stellate flounder are almost as frequent one way as the other. The number of sinistral individuals of the European flounder varies from 5 to 36 per cent in different localities and age groups. In the embryos of each of these species, however, the crossing of the optic nerve is uniformly monomorphic, either dextral or sinistral according to its kind. Many specimens reach maturity, therefore, with an over-twisted chiasma instead of the untwisted type. Population-counts of the European flounder at Plymouth indicate that the handicapped fish die at an earlier age than the others (Duncker, 1900). It is reasonable to argue from this that if a three-right-angled chiasma carries a higher mortality than a one-right-angled chiasma, the fact of twisting is itself a mechanical disadvantage. The normal vertebrate chiasma perhaps may carry somewhat of this handicap by virtue of its two-right-angles of twist. It is presumably to offset this structural weakness in the vertebrates that the complicated systems of sensory and motor decussations have evolved, leading to the contralateral control of each side of the body by the opposite side of the brain. This has sometimes led to anomalous results: a trout blinded in the right eye will darken on the left side of the body, which obviously can serve no useful purpose in protective adaptation (Frisch 1911).

THE PINEAL BODY

The mystery which has surrounded the pineal gland since the days of Descartes, who lodged therein the theological soul, has if anything been enhanced by the efforts of biologists (among them Gaskell in chief, 1908) who would discern in this rudimentary organ a leading clue to the gap between the invertebrate and vertebrate kingdoms. There are good reasons for considering the pineal-epithalamic complex on the roof of the third ventricle to be the enantiologue of the pituitary-hypothalamic complex on its floor. The pineal recess of the third ventricle corresponds to the hollow of the infundibulum; the glandular pineal body or epi-physis represents the neuro-pituitary or hypo-physis and, like that gland, has some part in the control of

sexual development; the habenular ganglion corresponds (at least in mammals) to the hypothalamus.

The surviving pineal eye (of lampreys and reptiles) is as distinct from the solid pineal gland (of birds and mammals) as the paired lateral eyes are distinct from the pituitary gland. No animal possesses both structures (glandular and visual) in its epithalamus; there has been a tendency, therefore, to regard all unpaired, midline structures in this position as homologues, and to say that the pineal gland of mammals is the representative or rudiment of the pineal eye of lower forms.

The life-story of the lamprey recapitulates in five years the early history of the vertebrate kingdom. The lamprey has in the roof of its head two pineal eyes, right and left, one of which (the left) has degenerated and rotated to the midline anteriorly, the other (the right) is functional and has rotated to the midline posteriorly. Each eye has or had a pineal optic nerve which passes into the habenular ganglion of its own side, and thence to the optical centres in the roof of the mid-brain. The two nerves, starting above from the eyes fore and aft, rotate as they descend and come to lie side by side: rotate, that is, to form a semi-chiasma of one right-angle (Gladstone, 1940). This is the condition reached (from the opposite direction) in the dextral flounder which untwists its optic chiasma.

The pineal eyes of the lamprey are a direct inheritance from its unknown invertebrate ancestors. This is proved by two salient facts. Invertebrate eyes, starting as an invagination of the outer skin, have the pigment-cells superficial, the nerve-cells deep—the so-called erect type of retina. Vertebrate eyes likewise start as a pigmentation and dimpling of the skin, close to the midline of the back; at a very early age (in the human, within three weeks of conception) the whole midline strip of skin is itself invaginated to form the neural tube, and the optic dimple or cup, increasing its depth, is now an evagination from the neural tube rather than an invagination from the skin. "The human optic pits are two lateral out-pouchings of the anterior end of the neural tube. Since the cephalic extremity of the tube is still open at the time of their formation they actually form ectodermal depressions on the surface of the body. When the roof of the neural tube is ultimately closed, these evaginations enlarge and... form two lateral projections on the ventro-lateral aspect of the brain (4 mm stage)" (Duke-Elder, 1932). Thus it grows toward the surface, nerve-cells or deep side first, and the retina is said to be inverted. The pineal eyes of the lamprey are erect, that is of invertebrate type, with the pigment cells superficial, the nerve cells deep.

Moreover, each pineal eye is connected to the habenular ganglion of its own side, as in the cuttlefish; there is no decussation and no contralateral control. The right habenular ganglion, of the lamprey corresponding to the surviving and functional eye, is much larger than the left. In reptiles, it is the left eye which functions, the right which degenerates; the left habenular ganglion accordingly is the larger, proving that control is predominantly ipselateral.

In its early larval stage, the lamprey has only pineal eyes, its epithalamus is in control of its daily cycle of color-change, and its hypothalamus and hypophysis are immature. Later it grows into the vertebral pattern, its lateral eyes develop and its pineal eyes undergo degeneration. Why this degeneration should occur in the lamprey and in all vertebrates is not known. A zenithal eye is not of great use; the pineal complex is buried by the overgrowth of the cerebral cortex; the skull-bones enlarge and thicken to give support to the temporal muscles that move the biting jaws: all these have been suggested and all may be true. It is more than likely that the pineal eyes, finding their outlook reversed after axial rotation, and the visual reflexes they control taking place all in the wrong direction, attempted a kind of neurobiotaxis to correct the error and to regain their wonted fields of view. In this the two eyes were successful only to the extent of one quarter of a turn; their half-completed journey, which brought them both to the midline-position, was never finished owing to their supercession by the lateral eyes on the other side of the brain. Whatever their fate, there is no doubt that the pineal and invertebrate eyes of the lamprey are embryologically, as they are racially, the earlier of the two systems.

The paired eyes, and their optic nerves which decussate at the chiasma, have been explained as having arisen in the earliest vertebrates as a consequence of axial rotation. It is remarkable, therefore, that the neural centres of the ventrally placed optic nerves are the same as those of the dorsally placed pineal nerves of the roof of the mid-brain: the optic fibres have to encircle almost the whole girth of the brain-stem, after leaving the chiasma, to arrive at their destination. A few of the visual afferents, however, succeed in making contact with the hypothalamus, just as the bulk of the pineal nerves enter the habenular ganglion, and this is a further reason for regarding the one system as the enantiologue of the other.

Both epithalamus and hypothalamus have intimate connections with the olfactory centres: the dorsal nuclei through the striae medullares, the ventral through the medial forebrain bundle. The division of the rhinencephalon itself into a degenerate dorsal half and a functioning ventral half may be related to the division of labor in the cross-brain resulting from axial rotation and the refashioning of the visual system, leaving the ventral hypothalamus functioning and the dorsal epithalamus degenerate.

CONTROL OF RHYTHM

The pineal gland of the epithalamus is the enantiologue of the pituitary gland of the hypothalamus. In the larval lamprey, the pineal complex controls the rhythm of the daily color-change from pale-by-night to dark-by-day; when it is removed, the animal remains dark. Not only does the pineal control the rhythmic response to the nyctohemeral rhythm, but it has also internalized this rhythm: when the animals are kept in total darkness "the diurnal changes usually persist, though diminished in extent" (Young, 1935). Removal of the pineal complex largely abolished this internalized rhythm.

In thus mediating the rhythmic response to day and night, and in internalizing the rhythm, the pineal complex of the lamprey shows its affinities both with the pituitary gland of the higher vertebrates and with the corresponding dorsal structure of insects. The paracardiac body of insects is a small knot of neuro-secretory tissue containing three types of cells: chromophil, chromophobe and interstitial. The chromophil cells are probably the source of a colloid substance resembling that in the mammalian hypothalamus; they provide the hormone responsible for color-change in certain insects. Closely associated with the paracardiac body is the corpus allatum which produces a "juvenile hormone," a yolk-forming hormone, and a hormone which has a general effect on metabolism, reminiscent of the polyvalance found in pituitary secretions. The greater part of the complex lies dorsally as regards the pharynx and the ventral nerve-cord.

Certain insects have the power of internalizing a rhythm. The stick-insect Dixippus is dark at night and pale by day, and this daily rhythm has been found to continue for several weeks in complete darkness; it is not inborn, for it fails to appear if the insect is hatched in darkness and kept in the dark. It is an acquired rhythm, and it can be reversed by artificial reversal of the rhythm of illumination; the reversed rhythm will persist in complete darkness just as the natural rhythm. The Chinese fire-fly *Luciola sinensis*, which regularly lights up at seven in the evening, keeps to this habit for several days when kept in the dark. The daily flashings of *Photinus pyralis*, another fire-fly, persist for at least four days. The cricket Gryllus shows a daily rhythm of general activity which will persist at least two weeks in continuous darkness at constant temperature and humidity; like so many others, its rhythm can be reversed by reversed illumination (Wigglesworth, 1950).

It is only an assumption that in insects the paracardiac system which controls the changes of color is the locus for the nyctohemeral rhythm and for the known faculty of internalizing this rhythm. In the crustacea, however, it is known for a fact that the sinus gland (physiologically the analogue of the pituitary) controls the daily rhythm. The fiddler-crab Uca is paler at night than by day, and can maintain this rhythm for as long as 25 days, whether in continued light or total darkness (Abramowitz, 1937); the rhythm is controlled by a glandular structure in the eye-stalk, characterized by blood-sinuses into which it discharges a pigmento-motor chemical resembling mammalian pituitrin. The sinus gland (as it is called) may be regarded as the crustacean equivalent of the pituitary, and there is evidence that it resembles the mammalian gland also in being responsible for calcium regulation and control of growth (Navez, 1934). When the sinus gland is removed (in Uca) the daily rhythm of its color-change is abolished (Abramowitz, 1937).

The reasons are familiar for believing that the human response to natural rhythms is located in the hypothalamus and pituitary. The centres for sleeping and waking are topographically identical (in the rat) with those of

the parasympathetic and orthosympathetic in the hypothalamus (Nauta 1946). Many experiments have been made on mammals to test their powers of internalizing the daily rhythm. The longest maintenance of an internal daily rhythm yet recorded was in the white-footed mouse, which kept up a well-defined alternation of activity and rest in an unchanging environment for eighteen months (Johnson, 1939).

The power of internalizing a rhythm is probably as specific a function as any in the nervous system, as characteristic of the tissues concerned as is vision of the eye, and hearing of the ears. In the insect this power resides in the dorsally placed paracardiac centres; in the vertebrate, in the ventrally placed hypothalamo-pituitary complex. Apart from the histological evidence, the imputed homology of these two systems of control is greatly strengthened by the location in both sites of the highly specific power of internalizing an environmental rhythm. The change of position from dorsal to ventral of this neuro-glandular complex is adduced therefore as further evidence for the theory of Axial Rotation.

The lamprey in its five years of adolescence recapitulates the lost story of the earliest vertebrates, in the change-over from dorsal to ventral systems of visual perception. The same animal exemplifies also the change from dorsal to ventral location of the neuro-chemical centres for responding to and internalizing the rhythms of the environment.

SUMMARY

1. Axial Rotation is postulated as the origin of the vertebrates, as this theory alone can account for the reversal from ventral to dorsal of the position of the nervous system.

2. The uncrossed visual control in the higher invertebrates is contrasted with the contralateral control in the vertebrates.

3. The optic chiasma of flat-fish undergoes certain changes during their axial rotation from upright to flat, and these are considered relevant to the theory.

4. The rise and fall of the pineal complex in vertebrate phylogeny is explained by this theory.

5. The enantiology of epithalamus and hypothalamus is related to that of the dorsal (degenerate) and ventral (functioning) halves of the rhinencephalon.

6. The glandular functions of the pineal complex are compared with those of the pituitary.

7. The dorsal pituitary of insects is compared with the ventral pituitary of vertebrates, especially in regard to the power of internalizing an environmental rhythm.

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APPROXIMATE CONFIDENCE INTERVALS FOR SPECIFIC LOCUS MUTATION RATES

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Point mutations, even in irradiated populations, generally occur with extremely small frequencies, and the most difficult obstacle for the average experimenter to overcome is that of obtaining enough data for his results to be meaningful. Because of the sheer number of animals required, very few specific locus mutation rate studies have been conducted and many of these have been restricted in scope. In recent years attention has been focused on the possibility that exposure to radioactive material might represent a hazard to man in terms of its effect on mutation rates. As a result mutation rate studies have been slowly increasing in numbers and in size, and the area of investigation has been extended to the mouse (Russell, 1951). As yet the mouse is the only mammal which has been studied systematically, and it has taken several years to obtain the data which are now available.

Enough data have been accumulated now so that geneticists have begun to make comparisons of radiation-induced mutation rates among species, and because of the urgent need for some estimate of human hazards, no matter how crude, the results are being used to make inferences about human populations. Russell (1951) compared mutation rates in mice and Drosophila on the basis of preliminary results from his own work and the existing literature on Drosophila. No tests of statistical significance were attempted at that time because of the lack of truly comparable data for the two species. Later Ives (1954) discussed the same problem and apparently reached a somewhat different concludion. Recently Russell (1956) has devoted an entire paper to this problem incorporating later data from his own study and new data on Drosophila including experiments (Alexander, 1954) which were specifically designed to provide data for comparison with the mouse. In this case it was possible to make a test of statistical significance. The test confirmed Russell's earlier conclusion that the specific locus mutation rate in the mouse is higher than in Drosophila. There is of course the additional problem of computing confidence limits for these mutation rates and this paper discusses a method for constructing such limits.

The construction of confidence intervals or limits of error for mutation rates obtained in experiments of this kind is complicated by the same factors which complicate the studies themselves. One quantity relevant to the assessment of the genetic effects of radiation is the mutation rate per locus for the population of loci at which mutations can occur in a given species. The number of loci is usually unknown although for most species which have been studied, it is estimated to be in the tens of thousands. Furthermore,

the number of known loci at which mutations have been observed is often quite small, and they are usually restricted to such readily observable characteristics as eye color, coat condition, shape of wings, etc. These considerations lead directly to the following two assumptions which would be required for any approach to the confidence interval problem:

(1) The number of loci in the sample is negligibly small compared to the number of loci in the population.

(2) The loci in the sample are chosen at random from the population of loci.

Assumption (1) is certainly satisfied in every case to be considered and means that for practical purposes the size of the locus population can be considered infinite. Assumption (2) is most certainly not satisfied since the loci studied in these experiments are those which have in the past been easily recognized. However, the real intent of assumption (2) is that the method of sampling loci should be such that loci with mutation rates which are either very large or very small, are not preferentially selected. A priori there is little reason to suspect that loci, which when mutated become manifest to the observer, have rates which differ from other loci. In other words there is no reason to suspect a correlation between the magnitude of the mutation rate at any locus and the observability of its phenotype. Thus assumption (2), though not strictly correct, may be accepted and in fact must be accepted if any attempt at constructing intervals is to be made.

If assumption (2) is not satisfied and the result is an upward bias in the point estimate, the effect would be present in any species studied so that species comparisons would presumably not be affected.

In what follows it will be assumed that N males have been exposed to the same dose of radiation and that each survivor is mated to several unirradiated females yielding a total of n offspring from each male. Each offspring is examined for mutations at each of k loci and x_i ($i = 1, \ldots, k$) mutations are found at the *ith* locus among all offspring examined. It is reasonable to assume that the conditional probability distribution of each x_i is of the Poisson form,

$$g(x|m) = \frac{m^x e^{-m}}{x!} \qquad (x = 0, 1, \ldots),$$

where m is the expected number of mutations at the locus being studied in a sample of Nn offspring. The distribution is conditional in the sense that x will have this distribution only if m is a constant. Actually in the present problem, m is itself a random sample from the population of loci and will have a probability distribution h(m), ($0 < m < \infty$). Since k is assumed to be negligibly small with respect to the number of loci in the population, h(m) may be assumed to be continuous. Then the unconditional probability distribution of x is

$$f(x) = \int_0^\infty g(x|m)\ h(m)dm.$$

The parameter for which an estimate is desired is the mean number of mutations in the population of loci, i.e.,

$$\lambda = \int_0^\infty m\, h(m)dm .$$

Furthermore the expected value of x is

$$\begin{aligned} E(x) &= \sum_{x=0}^{\infty} x\, f(x) \\ &= \sum_{x=0}^{\infty} x \int_0^\infty g(x|m)\, h(m)dm \\ &= \int_0^\infty h(m) \left[\sum_{x=0}^{\infty} x\, g(x|m) \right] dm \\ &= \int_0^\infty m\, h(m)dm \\ &= \lambda . \end{aligned}$$

Thus the number of mutations observed at any locus is an unbiased estimate of λ, and so is $\bar{x} = \sum_{i=1}^{k} x_i/k$. In other words, the observed mean number of mutations per locus is an unbiased estimate of the population parameter λ, irrespective of the form of the probability distributions, $g(x|m)$ and $h(m)$.

At first glance one might be tempted to construct a confidence interval for λ by assuming that the total number of mutations, $X = \sum_{i=1}^{k} x_i$, has a Poisson distribution. Clearly this procedure would lead to an interval which is too small, since it fails to incorporate the error imposed on the observed data by variations in the mutation rate at different loci. It includes only the Poisson error of sampling at each locus. The conclusion must be that X does not have a Poisson distribution, and any procedure for constructing confidence intervals based on the assumption that it does is incorrect.

In fact X has a distribution which depends on the unknown probability distribution, h(m), and any correct method must be based on some assumption about the form of this distribution. One of the most flexible continuous probability distributions for variables bounded between 0 and ∞ is the gamma distribution,

$$(1) \qquad \frac{1}{(\alpha - 1)!\, \beta^\alpha}\, m^{\alpha-1}\, e^{-m/\beta} .$$

This is a two-parameter distribution and is flexible in the sense that it can take many different shapes depending on the choice of the parameters α and β (Mood, 1950). With no information, experimental or theoretical, on which to base a decision, it would seem advisable to choose a distribution of this type for h(m) in the hope that a proper choice of α and β would produce a distribution close to the unknown true distribution. Thus if h(m) is taken equal to (1), the distribution of x is given by

$$f(x) = \int_0^\infty \frac{m^x e^{-m}}{x!} \cdot \frac{1}{(\alpha - 1)!\, \beta^\alpha} m^{\alpha-1} e^{-m/\beta}\, dm$$

$$= \frac{1}{x!\,(\alpha - 1)!\, \beta^\alpha} \cdot \frac{\Gamma(\alpha + x)}{\left(1 + \frac{1}{\beta}\right)^{\alpha + x}}$$

This distribution is often called the negative binomial distribution and is sometimes referred to as the Pascal distribution. More often it is found written in the form,

$$f(x) = \frac{\Gamma(\alpha + x)}{x!\, \Gamma(\alpha)} \left(\frac{\lambda}{\lambda + \alpha}\right)^x \left(1 + \frac{\lambda}{\alpha}\right)^{-\alpha}$$

where $\lambda = \alpha\beta$. In this form the mean of the distribution is λ and the parameter α is referred to as the exponent of the distribution.

In an effort to determine whether this distribution would adequately describe the results of mutation rate studies of the kind previously described, seven sets of published data were examined with this purpose in mind. Preliminary calculations indicated that the exponent in the distribution should be taken as one. In this case ($\alpha = 1$) the distribution has the form,

$$f(x) = \frac{\lambda^x}{(1 + \lambda)^{x+1}}. \tag{2}$$

The mean is λ and the variance is $\lambda(1 + \lambda)$. Thus from a sample of k loci, $x_1, x_2, \ldots, x_k$, the quantity

$$\chi^2 = \frac{\sum_{i=1}^{k} (x_i - \bar{x})^2}{\bar{x}(1 + \bar{x})},$$

where $\bar{x} = X/k$, has approximately a chi-square distribution with $(k - 1)$ degrees of freedom under the hypothesis that the sample is drawn from a population whose probability distribution is given by (2). This chi-square test was applied to the seven different sets of data and the results are shown in table 1. Excellent agreement with the hypothesis was found in five sets, and in the remaining two sets, the observed numbers of mutations varied less than would be expected on the basis of assuming (2) as the parent population. In practice then if (2) is assumed to be the correct

TABLE 1

CHI-SQUARE TESTS ON SPECIFIC LOCUS MUTATION DATA

Investigator	Russell (1951)		Alexander (1954)		Alexander (1954)		Patterson (1934)		Mickey (1954)		Mickey (1954)		Ives (1954)	
Material	Mouse Spermatogonia		Drosophila Spermatogonia		Drosophila Sperm		Drosophila Sperm		Drosophila Sperm		Drosophila Sperm		Drosophila Sperm	
Radiation	X-ray		X-ray		X-ray		X-ray		X-ray		Neutron		X-ray	
	L*	#†	L	#	L	#	L	#	L	#	L	#	L	#
	A	0	ru	0	ru	5	ru	16	ru	3	ru	2		
	B	9	h	2	h	6	h	1	h	1	h	2	h	1
	C	3	th	0	th	4	th	3	th	2	th	1	th	2
	D	6	st	0	st	10	st	8	st	3	st	0	st	6
Number of	P	7	pP	0	pP	13	cu	3	pP	2	pP	3	pP	5
Mutations	S	22	cu	2	cu	8	sr	4	cu	3	cu	3	cu	6
	Se	0	sr	3	sr	12	e^s	13	sr	7	sr	1	sr	13
			e^s	3	e^s	13	ca	22	e^s	11	e^s	3	e^s	6
Mean $\bar{x}$	6.71		1.25		8.88		8.75		4.00		1.88		5.57	
$\sum(x-\bar{x})^2$	343.43		13.50		92.88		395.50		78.00		8.88		89.71	
$\bar{x}(1+\bar{x})$	51.796		2.813		87.641		85.300		20.000		5.391		36.612	
χ^2	6.630		4.799		1.060		4.637		3.900		1.646		2.450	
P‡	0.37		0.68		>0.99		0.70		0.79		0.97		0.87	

*L = locus
†# = No. of mutations at corresponding locus
‡P = probability of a greater value of chi-square

distribution, it appears that confidence intervals computed therefrom will be correct in most cases, and when not correct will be too large. The latter conclusion follows directly from the observation that in two sets of data, the distribution assumed would actually have a larger variance than is indicated. In no case was the variance smaller than expected. This conservative approach is clearly preferable to the aforementioned method based on Poisson variability which uniformly would give confidence intervals which are too narrow.

If the number (x_i) of mutations at the *ith* locus has the distribution given by (2), i.e., a negative binomial distribution with a mean of λ and an exponent of one, then $X = \sum_{i=1}^{k} x_i$ is known to have a negative binomial distribution with a mean $k\lambda$ and an exponent k (Anscombe, 1950). Furthermore, Anscombe (1948) has shown that for this distribution when k is known, the transformation

$$y = \sinh^{-1}\left(\frac{X + 3/8}{k - 3/4}\right)^{1/2} \tag{3}$$

has certain desirable properties. In particular the variable y will be approximately normally distributed when $k > 2$ and $k\lambda$ is large. The variance of y is approximately $1/4(k-1)$. These properties may be used to place confidence limits on the transformed variable, and the limits so obtained may be transformed back to provide limits for $k\lambda$. Specifically if we take

$$\text{Upper limit} = y_U = \sinh^{-1}\left(\frac{X + 3/8}{k - 3/4}\right)^{1/2} + 2\left[\frac{1}{4(k-1)}\right]^{1/2}$$

$$\text{Lower limit} = y_L = \sinh^{-1}\left(\frac{X + 3/8}{k - 3/4}\right)^{1/2} - 2\left[\frac{1}{4(k-1)}\right]^{1/2}$$

then the approximate 95 percent confidence limits for $k\lambda$ would be given by

$$X_U = (k - 3/4)\sinh^2 y_U - 3/8$$

$$X_L = (k - 3/4)\sinh^2 y_L - 3/8.$$

The method may be illustrated with Russell's (1951) data on the spermatogonia mutation rate in mice as given in table 1. The total number of mutations at all seven loci is 47, so that $X = 47$, $k = 7$. From formula (3),

$$y = \sinh^{-1}\left(\frac{47 + 3/8}{7 - 3/4}\right)^{1/2} = 1.7374,$$

and the standard deviation of y is

$$\left[\frac{1}{4(7-1)}\right]^{1/2} = 0.2041.$$

Thus

$$y_U = 1.7374 + 2(0.2041) = 2.1456$$

$$y_L = 1.7374 - 2(0.2041) = 1.3292,$$

whereupon,

$$X_U = (7 - 3/4)\sinh^2(2.1456) - 3/8 = 110.67$$

$$X_L = (7 - 3/4)\sinh^2(1.3292) - 3/8 = 18.91.$$

These are the approximate 95 percent confidence limits on the total number of mutations. The experiment was performed with 600r of X-radiation and a total of 48,007 spermatogonia were tested. Thus the point estimate of the experimental mutation rate/r/locus is

$$\frac{47}{7 \times 600 \times 48{,}007} = 23.3 \times 10^{-8},$$

(This figure differs slightly from the figure of 22.1×10^{-8} given by Russell (1956) since he is quoting the induced rate whereas the value given here is not corrected for spontaneous mutations. Alexander (1954) found no spontaneous mutations so that the Drosophila rate given below agrees with that quoted by Russell.) and the approximate 95 percent confidence limits are

$$\frac{18.91}{7 \times 600 \times 48{,}007} = 9.4 \times 10^{-8}$$

and

$$\frac{110.67}{7 \times 600 \times 48{,}007} = 54.9 \times 10^{-8}.$$

Identical calculations with the Drosophila spermatogonia data of Alexander (1954), also shown in table 1, yield a point estimate of 1.52×10^{-8} with 95 percent confidence limits of 0.45×10^{-8} and 3.85×10^{-8}.

The primary purpose of this paper is to present a reasonable basis for the computation of confidence limits from specific locus mutation rate studies. The method proposed has been justified in part by reference to known properties of the sampling errors in mutation numbers, and in part by a test of the model with seven independent sets of data. It has been emphasized that the confidence limits obtained are only approximate and Anscombe (1948) has shown that the estimates may be as much as 10 percent too low as a result of the inverse transformation of y_U and y_L. Nevertheless the method is certainly better than one based on Poisson errors alone, and when limits from two different experiments are compared, as for example, the experiments of Russell (1956) and Alexander (1954) already mentioned, the failure of the 95 percent confidence intervals to overlap should leave little doubt about the significance of the higher mutation rate in the mouse. This is particularly true because the assumptions made tend if anything to produce confidence intervals which are wider than the correct ones. It should be noted that the result of this comparison adds further strength to the test of statistical significance made by Russell (1956) and referred to in an earlier paragraph.

A further point to be made is that the appearance of a locus with an apparently high rate is to be expected in any distribution which results from the compounding of Poisson populations with different means, whether or not the resulting distribution is a negative binomial. In other words the observed variability should be greater than one would expect in sampling from a single Poisson population, and the results in table 1 clearly support this observation. Thus any criticism, such as Ives' (1954), of the observed mutation rate in mice which is based on the contention that any specific locus with a high mutation rate is anomalous can hardly be supported. It is worth noting that even the data presented by Ives (1954) contain a locus (stripe) with a relatively high frequency of mutations and thus fall into the expected pattern.

ACKNOWLEDGMENT

The author is grateful to Dr. W. L. Russell for many helpful discussions during the preparation of this paper.

SUMMARY

A method is proposed for constructing approximate confidence intervals for specific locus mutation rates. The assumptions on which the method is based have been tested by an analysis of published data on mutation rates, and the results of the analysis indicate that the assumptions are conservative. This implies that if the method is in error, it will lead to confidence intervals which are too large rather than too small. The method is applied to data from radiation experiments with Drosophila and mice, and the results

support a conclusion made by Russell (1951, 1956) that the spermatogonia mutation rate in mice is higher than the spermatogonia mutation rate in Drosophila.

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INDUCTION OF MUTATIONS BY FORMALDEHYDE SOLUTIONS IN *DROSOPHILA MELANOGASTER*

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So far the only effective methods of inducing mutations by formaldehyde treatment in Drosophila germ cells are either by mixing the chemical with the food of the larvae, or by injecting the solution in the body of the adult fly (Auerbach, 1952 and 1953, and Sobels 1954). In the feeding method, the effectiveness of the mutagen can only be tested on the larval germ cells, as attempts to feed adults on formaldehyde-treated food proved to be unsuccessfull. Consequently, the pattern of sensitivity of the germ cells to the mutagenic action of formaldehyde has been but partly determined, mainly by Auerbach. However, the introduction of the mutagen through the alimentary canal has its drawbacks. On the one hand, one can never be sure whether the effect produced is directly due to the chemical used without being changed through reactions with other groups. On the other hand, by the application of the feeding method it is not possible to test for the effectiveness of the mutagen or the sensitivity of the germ cells during the pupal life. Such a test is of importance, as it was shown for X-rays that the most sensitive stage of spermatogenesis occurs during late pupal life, (Khishin 1955).

By the second method, that of injecting the solution into the adult fly, it may not be possible to detect a more sensitive stage than the mature spermatozoa by using the usual brood technique. This is so, for reasons which depend almost entirely on the handling of the flies, and on the mating procedure after treatment. Factors such as the number of females per single male, the brood interval, the type of food used, and many others may conceal—as in fact they did in the past—the sensitive stage. All these factors affect the rate of flow of the spermatozoa, so that the sensitive stage may be diluted, to a greater or lesser degree, by stages of lower sensitivity.

For these reasons the present set of experiments was planned. Formaldehyde is being applied in the form of aqueous solutions, in which different pre-imaginal stages of *Drosophila melanogaster* are simply immersed. Different concentrations of the formaldehyde, and varying length of treatments are tested. This method is being tried on two embryonic stages, two larval instars, and on prepupae and pupae at various degrees of development. The aim is to establish the pattern of sensitivity to the formaldehyde by using the induced recessive sex-linked lethal mutations as the measure of sensitivity, and comparing the results obtained in the first broods of males treated at the above mentioned stages.

The present communication gives the result of an experiment in which formaldehyde solution was applied to pupae.

MATERIAL AND METHODS: The stock used was a wild type Or-K stock. The stage treated was that which after X-radiation gave the highest rate of recessive sex-linked lethals. This stage is about 174 hours from the time of egg laying, (see Khishin 1955). The formaldehyde used was a 40 percent commercial product, and dilutions were made with distilled water.

The treatment consisted of simply immersing the pupae in the suitable concentration of formaldehyde for a certain period. Pupae are kept well immersed into the solution by the aid of a piece of cotton wool itself pushed down under the surface. This is necessary as the pupae tend to float on the surface. After treatment the pupae were washed in several changes of tap water, then transferred into empty vials. A piece of filter paper or cotton wool supplies the necessary moisture and prevents drying.

The limits of the concentration of the formaldehyde solution or the duration of treatment will appear elsewhere. The present treatment, however, was for a period of three hours in 10 percent formaldehyde. With this period of treatment, and concentration of formaldehyde, we got about 50 per cent emergence, and almost all the emerging males were completely fertile.

The emerging males were then tested for the recessive sex-linked lethals by the well known Muller-5 technique. Each male was given two virgin Muller-5 females. Only the first brood was obtained, the brood period being three days. The Muller-5 method was also used to test for the spontaneous rate of sex-linked lethals in the stock. Although the spontaneous rate of mutations had been determined often at the Institute of Animal Genetics, Edinburgh, from which the stock was obtained, it nevertheless, was thought better to retest it under its new environment in Egypt.

RESULTS

The results of the experiment are given in the following tables.

TABLE 1

THE SPONTANEOUS RATE OF RECESSIVE SEX-LINKED LETHALS (OR-K).

No. males tested	No. of Chrom.	No. of Lethals	Lethals %
42	660	2	0.30

TABLE 2

THE RATE OF RECESSIVE SEX-LINKED LETHALS INDUCED IN THE GERM CELLS OF DROSOPHILA MALES TREATED AS PUPAE WITH FORMALDEHYDE

No. males tested	No. of Chrom.	No. of Lethals	Lethals %
45	600	8	1.33

CHI-SQUARE TEST

The χ^2 for the result of the spontaneous and the treated series has a value of 4.24. This value indicates a significant difference at the 5 per cent level.

Thus it seems that this method of immersing pupae in formaldehyde solution is effective in producing sex-linked lethal mutations in the male germ cells of *Drosophila melanogaster*. However, the mutation rate is very low, although it is significantly higher than the spontaneous rate as shown by the χ^2 value. The result of the experiment also showed that the spontaneous rate of mutations did not change under the new conditions.

DISCUSSION

There are a few points of importance one has to remember when interpreting results of this kind. First of all, the rate of mutations induced in the germ cells will no doubt depend to a degree on the concentration of the mutagen that reaches the gonads. This in turn will depend on various factors, the most important of which are the length of treatment and the permeability of the puparium and the other internal tissues and cells. The temperature during treatment should also be expected to affect the results, primarily due to its effect on permeability.

Although the above results indicate the possibility of inducing mutations in the germ cells by immersion in formaldehyde solutions, yet to establish a sensitivity pattern by this method one has to overcome a great difficulty. The desire is to compare mutation rates induced in various stages of spermatogenesis after treatment with formaldehyde. But the various stages of germ cell development occur in more than one phase of the animal. For that reason it is necessary to treat eggs, larvae, prepupae and pupae, and also to treat more than one age within every stage. These different stages differ also in the nature of their outer coverings, the chorion of the eggs, the cuticle of the various larval instars, and the puparium of the prepupae and pupae. Consequently it is reasonable to expect differences in permeability through these outer layers. Besides, the internal tissues and/or aggregates of cells and their physicochemical nature also vary from the egg to the larvae and from the larvae to the pupae, and possibly also within the one stage. All this makes it inaccurate to immerse eggs, larvae and pupae in a certain concentration of the mutagen and then consider the rates of mutations induced as a measure of the differential sensitivity of the germ cells. The comparison will not be correct because the amount and concentration of the mutagen reaching the germ cells will not be the same in the three developmental stages, and possibly also within the same stage.

A possible way of overcoming these difficulties is by a good chemical estimation of the formaldehyde in the testes of samples taken from the treated material. If this could be done quantitatively, then it may be possible to interpret the results on the basis of the concentration of the mutagen in the testis. However, the difficulty now will be to find a quick, easy and sensitive chemical method for the estimation of formaldehyde in

the testes. So far, we have tried Schiff's reagent and diphenylamine in concentrated sulphuric acid, merely to test for the presence of formaldehyde in the testis of the treated pupae. Both methods gave negative results.

However, some chemical methods are now being tried, and a technique is being developed to ensure better penetration of the mutagen in the hope of obtaining higher rates of mutations.

SUMMARY

It was possible to induce recessive sex-linked lethal mutations in Drosophila male germ cells by simply immersing pupae in aqueous solutions of formaldehyde.

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BOOK REVIEW

MUTUAL AID AND EVOLUTION

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It is good to see Kropotkin's articles on Mutual Aid, first published in *The Nineteenth Century* between 1890 and 1896, and in book form in 1902, brought again to the attention of students of evolution. With all its faults it is a great human document, an expression of the indignation, shared by many and clearly and popularly expressed by Kropotkin, which is aroused when man is viewed as a creature formed by struggle against his fellows, and when his institutions and societies are seen as results primarily of this struggle. It was T. H. Huxley's essay on "The Struggle for Existence in Human Society" published in *The Nineteenth Century* in February 1888 which aroused Kropotkin's indignation and his articles and later book (it is the 1914 edition with its preface which is now reprinted) were direct replies to Huxley's essay.

For comparison with this re-issue I took down my copy of the original edition of 1902 of Mutual Aid which I read as a student over 40 years ago. My notes recalled the impression it had made upon me, for I too was troubled by the antithesis in man's nature, and had been led to Kropotkin by Graham Wallas' *The Great Society* which I read in the same year 1914. To look at those two books now is to see as in a mirror the young man with that time as a background. Then I saw dimly what seems clearer now—that both views, Kropotkin's and Huxley's, were incomplete and distorted because they confused scientific with moral or ethical questions, and tried to justify their views on both from the same evidence. There are many causes of this confusion. "Aid" and "struggle" appear where we use them in a narrow, anthropomorphic sense to be transitive verbs which imply the kind of consciousness (our own) which seems driven to form ethical judgements. It is an all too common practice for those who aim at objective views justified by the facts and the reasoning method of natural science to use such words without precision and to attribute to a natural process such as evolution meanings and motivating forces which are expressions of human (and often humane) aspirations and fears. Surely we should not adduce the behavior of such stereotyped automata as ants or their societies as evidence for either view; nor should we, as Huxley did, preface our arguments "I am as strongly convinced as the most pronounced individualist can be—." Kropotkin's use of the evidence was determined by his philosophical posi-

*Mutual Aid, by P. Kropotkin, introduction by Ashley Montagu with an appendix: The struggle for existence in human society, by Thomas H. Huxley. Extending Horizons Press, Boston, Mass., 1955, 362 pp. cloth bound $3.00, paper bound $2.00.

tion as an anarchist for whom cooperation was a substitute for the State, while Huxley's thoroughgoing and unabashed materialism led him to admire equally (so he said) the wolf and its victim the deer. But it is clear that his sympathies were with the winner.

It gives one pause to reflect how one set of facts, observations generally agreed to, like those underlying the theory of natural selection, may lead in different minds to divergent and irreconcilable meanings. Does the reason for this lie in the different extraneous or personal circumstances under which the bent or set of the mind is formed? And how, if this be an ever present danger, is the ultimate disaster to science to be avoided, whereby the discourse is put upon a plane where decision by reference to the factual observations is impossible? One suspects this happens often in the history of science, and that the struggle to limit the meaning of words precisely to the point requiring decision is far from won.

In perspective the final question remains: what have these differing attitudes of Kropotkin and Huxley to do with the scientific study of evolution? Obviously the answer is nothing, if we speak of factual observation, but everything if we mean interpretation. I think it can be said that neither Kropotkin nor Huxley contributed much to the understanding of the mechanism of evolution by natural selection. The firm foundation for this was laid by the more sober work of Darwin and Wallace. After their work was done, neither one of these men concealed their mature and deeply moral views, but they did not derive them from the evidence for organic evolution. Darwin's views are well-known from the attitudes expressed in his letters. The last paragraph in Wallace's *Darwinism* (1889, page 478) is less widely known: "We thus find that the Darwinian theory, even when carried out to its extreme logical conclusion, not only does not oppose, but lends a decided support to, a belief in the spiritual nature of man. It shows us how man's body may have been developed from that of a lower animal form under the law of natural selection; but it also teaches us that we possess intellectual and moral faculties which could not have been so developed but must have had another origin; and for this origin we can only find an adequate cause in the unseen universe of Spirit". And only recently have I encountered for the first time (quoted by S. F. Mason in Centaurus 1953: Vol. 3, pp. 90–106) this sentence of Wallace published in 1900: "The only mode of natural selection that can act alike on physical, mental and moral qualities will come into play under a social system which gives equal opportunity of culture, leisure and happiness to every individual". This is a statement, not of fact, but of the same hope which motivated Kropotkin. The moral position of each man was an acquired character, influenced in each case by many factors beyond the facts of evolution accessible to both of them.

T. H. Huxley's position to which Kropotkin was so strongly opposed, was made perfectly clear in his Romanes lecture of 1893. "The ethical progress of society consists, not in imitating the cosmic process, still less in

running away from it, but in combating it." It was Huxley's characterization of the cosmic (evolutionary) process as a "dog-eat-dog" affair against which Kropotkin's ire and opposition were aroused, and for which he tried to substitute his ethical idea of mutual aid, buttressed by evidence of cooperation in animal societies. Although T. H. Huxley occasionally justified his ethical views by his reasoning as a scientist, he did not try to derive them from evolutionary evidence. This remained for his grandson to do fifty years later (J. S. Huxley, Evolutionary Ethics, the Romanes Lecture, Oxford 1943); but the impression left by that attempt was that if one tries to derive today's ethics from evolutionary principles, he ends up by seeing its highest achievement in human societies of today and ascribing to the evolutionary process itself an ethical purpose. And this takes us out of the realm of science and into that unseen universe of belief into which Wallace, with more simplicity and directness, retreated.

These thoughts are not intended to belittle the achievements of Kropotkin or of Huxley or their followers in the last century or in this one. They faced our common dilemma and chose their sides; and since the processes of reason by which we all must live, are forwarded by defining alternatives and putting forward the issues to be clarified, we owe for this real service our thanks to all of those concerned in this controversy and to Professor Ashley Montagu for again calling it to our attention.

LETTERS TO THE EDITORS

Correspondents alone are responsible for statements and opinions expressed. Letters are dated when received in the editorial office.

COMMENTS ON PROFESSOR LEWONTIN'S ARTICLE

The validity of the ideas and conclusions expressed by Professor Lewontin in his interesting and stimulating article appearing in the July issue of this Journal does not depend on the some-what novel definition he chooses to adopt of the term homeostasis; the definition may, however, lead to some confusion in comparisons of his ideas with those of others. Lewontin writes, in the section entitled *Definition of homeostasis*, "Operationally, then, one genotype is defined as being more homeostatic than another if its mean adaptive value is higher in the specified environmental range." And in the second section following he argues, in comparing two genotypes hypothesized for illustrative purposes, the one with the higher mean but more variable adaptive value is more homeostatic since "if homeostasis is to be any measure of the evolutionary future of a genotype, of the capacity of a genotype to adapt on the average to varying environment, no other result seems permissible."

While "adaptive value" and "homeostasis" seem almost equated by this definition and example, they do have the merit of forcefully directing attention to the role of variable environment. But, etymologically considered, homeostasis clearly and almost redundantly indicates constancy, and constancy is central in Cannon's use of the term. He has written (pages 23, 24, and 25 of *The Wisdom of the Body*, 1932): "The perfection of the process of holding a *stable state* in spite of extensive shifts of outer circumstance is not a special gift bestowed upon the highest organisms but is the consequence of a gradual evolution. . . . The coordinated physiological processes which maintain most of the *steady states* in the organism are so complex and so peculiar to living beings—involving, as they may, the brain and nerves, the heart, lungs, kidneys and spleen, all working cooperatively—that I have suggested a special designation for these states, *homeostasis*. The word means a *condition*—a condition which may vary, but which is *relatively constant*." [Most italics mine] It seems clear, here and in the remainder of his book, that homeostasis applies to particular *conditions* that are maintained in a *relatively stable state* by special mechanisms that have been evolved through natural selection; whereas the causative conditions, which are themselves variable, are called homeostatic devices or mechanisms (see for example chapter 11). As Cannon has used the term, homeostatic conditions seem important aids to, or compo-

nents of, fitness, but not fitness itself; any particular organism, no matter how effective might be its homeostatic mechanisms, could conceivably possess flaws in other respects greatly reducing its fitness. Thus Cannon would not, I feel sure, consider homeostasis to be, as Lewontin assumes, a "measure of the evolutionary future of a genotype".

Lewontin's emphasis that natural selection sometimes favors variability as an adaptive character is timely and pertinent with respect to current discussions of homeostasis. As illustration he points to devices leading to homeostasis in body temperature of homoiotherms. Dilation of the peripheral blood vessels varies widely in response to changes in external temperature, a lability that adds to fitness. Cannon does not call degree of dilation a homeostatic character; since it is an aid to fitness, perhaps Lewontin does. Probably the divergence between Cannon's and Lewontin's definitions arises chiefly because the latter applies the term to organisms, whereas Cannon applies it to conditions in *an* organism.

Cannon also considered an extension of the homeostasis concept to conditions of stability in social institutions. It therefore seems modest and reasonable to apply the concept, as Lewontin and others have done, to certain aspects of morphology or functions that are determined in the course of embryogeny. Some such characters would, no doubt, tend to be greatly modified in their development by environmental vicissitudes were it not for special regulative mechanisms that have arisen through the agency of natural selection. Lewontin's discussion, however, brings clearly to view some of the difficulties in testing the hypothesis that homeostasis of developmental characters of this kind is favored by heterozygosis. It is perhaps harder to select appropriate characters for test, than to test them once selected.

Lerner's term genetic homeostasis, which is a further extension of the concept to populations and refers to their relative stability under continued selective breeding, may well be consonant with the spirit of Cannon's usage. The stabilities referred to by Lerner are active properties of the populations, not mere exhaustion of genetic variance; and the mechanisms responsible, although only vaguely understood at present, may well have developed, in part at least, through the influence of natural selection.

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March 9, 1956

A REPLY TO PROFESSOR DEMPSTER'S COMMENTS ON HOMEOSTASIS

Professor Dempster has been kind enough to comment on what he feels are some confusing points in my discussion of homeostasis. The major point of disagreement between us seems to be, whether the definition of homeostasis I have proposed is consonant with the original meaning of the concept as used by Cannon.

Cannon's thesis is summed up clearly by Dempster when he says, "homeostasis applies to particular conditions that are maintained in a *relatively stable state* by special mechanisms that have been evolved through natural selection; whereas the causative conditions, which are themselves variable, are called homeostatic devices or mechanisms". The problem arises when one tries to specify the "particular conditions that are maintained in a *relatively stable state*" as opposed to the "causative conditions, which are themselves variable". By what sign shall we know the conditions which are to be kept constant? The answer to this question lies in the reference to natural selection. If homeostatic mechanisms are established by natural selection it is because their establishment results in an increase in fitness of the system possessing them. The conditions which are maintained in a steady state are, then, those whose stability confers a greater degree of fitness. Conversely, any conditions or mechanisms whose variability increases fitness will also be selected and established. If one wishes to measure relative degrees of homeostasis by the stability or variability of some conditions or process, it is essential to know whether that stability or variability confers a greater degree of fitness on the system being studied. An increase in homeostasis, then, results in an increase in average fitness. If this were not the case, homeostasis could not be the product of natural selection. It is just because Cannon recognized homeostasis as a product of evolution, that only an adaptive constancy can be considered as evidence of homeostasis.

The question arises as to whether an increase in adaptive value is a necessary and sufficient criterion of an increase in homeostasis. Dempster believes not for he states that "any particular organism, no matter how effective its homeostatic mechanisms, could conceivably possess flaws in other respects greatly reducing its fitness." It is this proposition which lies at the base of our lack of agreement. In my view, the dichotomy between conditions of the organism which lie within the framework of its homeostatic adjustment, and those which lie without, does not exist. There is no aspect of the physiology or morphology of an organism which is not concerned in its homeostatic adjustment. Protoplasm is an unstable system. A constant input of energy is required just to maintain it, for when this input of energy fails, the system degenerates. Any surplus of energy, over and above that needed for simple maintenance is devoted to increase of the system through its own growth and by means of leaving progeny. The total resources of an organism are devoted to these two ends, which are the two components of fitness. Natural selection leads according to Cannon, to the establishment of a relation among the various physiological processes which will assure the maintenance of protoplasm under the widest variety of circumstances. We have extended this concept to include the other component of fitness, capacity to increase. With this extension, it is not possible to conceive of a physiological or morphogenetic process which is not intimately woven into the fabric of homeostatic adjustment.

If these arguments be granted, then an increase in homeostatic adjustment leads ineluctably to an increase in average fitness. Conversely an increase in *average* fitness can result only from greater homeostatic adjustment.

As a last point, Dempster raises the question of Lerner's "genetic homeostasis". We are in agreement that the tendency of a population not to change its genetic composition too suddenly in the face of new selective forces, may indeed be adaptive. The point should be made, however, that this resistance may also be disastrous. Again, conservatism *per se* is not homeostasis. It is only a conservatism with an adaptive consequence which can be regarded as homeostasis.

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TAXONOMIC CRITERIA IN AUSTRALIAN FROGS

It is of interest at times to examine a particular original paper in respect to its contained procedures, interpretations, and implications, especially when the paper is referred to in general argument. Accordingly, the following review has been occasioned by the citations of Brown and Wilson (1954) and Moore (1955) of work by the latter on Australian frogs as illustrative of reproductive incompatibility between populations without morphological differences.

The appositely named *Crinia insignifera* was described by Moore (1954) from individuals which would formerly have been called *Crinia signifera* on the basis of incompatible crosses between two males from near Perth, West Australia, and two females from Sydney, New South Wales. Twenty-one per cent of the embryos from one of these crosses developed into swimming larvae apparently capable of metamorphosis. A third West Australian male yielded sperm which fertilized the eggs of two Sydney females. These eggs developed into "nearly normal" embryos and "healthy" tadpoles, some of which "were kept until they underwent metamorphosis into seemingly normal frogs." Reciprocal crosses were not made, and in no case was the actual number of eggs or young mentioned.

From this evidence alone, Moore stated that "genetic divergence has reached a point where the two populations should be recognized as separate species." No constant morphological differences were found between the new species from southwestern Australia and the populations which retained the name *C. signifera*. It was noted, however, ther there is considerable geographic variation and local polymorphism. No indication was given of the nature of this variation nor were data presented to support the assertion of no constant morphological differences. No mention was made of the number of specimens compared.

There seems to be little published information on normal habits of *Crinia signifera*, but one might expect the breeding season in Western Australia to coincide with the rainy season, which is sharply delimited at Perth in contrast to the more even annual precipitation pattern at Sydney on the eastern side of the continent. If this supposition is correct, the type of the new species (and presumably the other West Australian males used in the experiments) was collected after or near the end of the normal breeding period. Since the dates and most of the conditions of the experiments were not given, the bearing this may have on the results obtained must be speculative.

Moore postulated that the range of *C. insignifera* was the southwestern segment of the continent, isolated by arid areas from that of *C. signifera*, which was restricted to northern West Australia east to Queensland and south to South Australia, Victoria, and Tasmania. His interpretation may be correct, but it seems based on far too little experimental data, the populations concerned not being adequately sampled, especially for a species showing considerable local polymorphism.

If the data do reflect natural conditions in these populations, they may be explained on the basis of differences correlated with the extent of geographic separation when the range was continuous. Such differences might be adaptive or simply due to distance (Wright, 1940). The present geographic isolation, which seems to furnish in part a reason for considering the two populations as distinct entities, poses the commonly occurring taxonomic question of degree of difference. Moore reported only partial incompatibility which, to us, may well mean conspecificity, considering the distance involved. It is perhpas significant in this connection that three crosses of Tasmanian and New South Wales frogs produced normal young only. Although the Tasmanian population has quite possibly been isolated from that of New South Wales for about the same length of time as has that of southwestern Australia (*cf.* Gentilli, 1949), the geographic separation in the former case is far less. In addition to confirmation of the present results, it would appear very pertinent to cross frogs from many other localities, and particularly some from northern West Australia with others from southwestern West Australia and from South Wales or Victoria.

The work reported in the same paper by Moore on the Australian *Hyla aurea* and *raniformis*, in which morphological differences between populations are known, is open to somewhat similar questions.

Thus, in view of the paucity of information on the morphological (and ecological) characters and on their geographic variations in *Crinia signifera* and *insignifera*, the results of *partial* incompatibility reported, the possible relationship between extent of separation and these results, and the lack of comparable cases of such species adequately demonstrated among other vertebrates, it would seem to behoove biologists to consider circumspectly the status of the new species of *Crinia*. The dangers in doing otherwise lie not so much in agreeing with Moore's interpretation in this particular case

as in uncritically citing such work and in tacitly approving of the practices used in this instance for the establishment of vertebrate taxa, whether on "biological", ethological, or morphological grounds. The use of "biological" characters does not exempt a worker from consideration of *populations* and their characteristics.

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JAMES E. MOSIMANN

March 31, 1956

A REJOINDER TO RABB AND MOSIMANN'S LETTER

The questions raised by Rabb and Mosimann are of two sorts, namely, the interpretation of the data and the adequacy of the data. I will attempt to answer them in that order.

When certain frogs from Western Australia and New South Wales that belong to the same morphological species (*Crinia signifera*) are crossed, the hybrids show relatively specific types of defects. In different crosses the degree of defectiveness varies: in some crosses the developmental crises are passed and most of the embryos continue in their development; in other crosses most of the embryos die. I interpreted these data to indicate that two species are involved. The reason for so doing is that, in all the experiments on frog hybridization known to me (with the exception of the complex *Rana pipiens* situation where the taxonomic allocation of some geographic populations is a matter of arbitrary personal preference), such hybrid inviability is always associated with crosses of frogs belonging to unquestionably different morphological species. Rabb and Mosimann emphasize the "*partial* incompatibility which, to us, may well mean conspecificity...." Since it is impossible to obtain the most critical information to decide this point, namely, how the two populations of Crinia would behave if sympatric, I think the best we can do is to reason by analogy with what happens in crosses of other amphibians. If we do this the answer is reasonably clear: two species are involved.

So far as the adequacy of the data is concerned, I should first like to make one general observation. When defects are observed in the offspring from crosses of individuals of different populations of frogs, one is dealing with genetic differences of a considerable magnitude. These results are never encountered in crosses of individuals of the same species and sometimes not even in crosses of two morphological species. Furthermore, the results are usually so consistent that a few crosses are sufficient. In the four crosses of Western Australia males (of which there were three, not two as Rabb and Mosimann state) and New South Wales females that I was able to perform, the same type of defects were noticed in each, though the severity varied. The numbers of embryos used in the 4 crosses of New South Wales and Western Australia individuals were about equal in each and totalled 119 controls (N.S.W. × N.S.W.) and 183 hybrids.

Rabb and Mosimann are quite correct in surmising that my Western Australian males were collected near the end of the breeding season in Western Australia. However, the males were calling and they were collected at night in their breeding sites. This should ensure normal males. I used the males with confidence because in none of hundreds of crosses involving dozens of different amphibian species have I found the sperm of males collected in nature to be abnormal. Conceivably the sperm might be absent (though I have never observed this) and hence no fertilization could be expected. If sperm are present, and they certainly were in the males that I used, it is difficult to see how the time of their formation could have adversely affected their genetics.

The criticisms contained in the fifth paragraph of Rabb and Mosimann's letter are rather unfair since they belabor me for things I never said. So far as the individuals from Western Australia are concerned I wrote "Unless further experimentation proves it otherwise, we can regard all the frogs of south-west Australia, formerly known as *Crinia signifera*, as being *Crinia insignifera*." With respect to the other populations, I crossed individuals from central Tasmania, Kosciusko, and Sydney, New South Wales and, finding no cross-abnormalities, concluded on this evidence and on the absence of appreciable morphological differences, that a single species is involved. I had no material from Queensland, Northern Territory, or northern Western Australia and offered no verdict on the status of individuals from these states.

I cannot understand the criticism of paragraph six where Rabb and Mosimann write, "Such differences might be adaptive or simply due to distance." I fail to see how genetic differences can be due to distance. Presumably genetic differences are due to selection of mutations and possibly to genetic drift. Distance is not a cause of divergence though it may be associated with divergence. In any event 'differences are differences' and, if they serve as isolating mechanisms, it is immaterial how they arose.

There is a "paucity of information on the morphological (and ecological) characters and on their geographic variations" in my paper, as Rabb and Mosimann say. But my paper was not a monograph on the morphology and

ecology of these frogs. These data are available and they will be presented in due time. Unless the two species were sympatric, data on any differences in ecology would be of limited value. So far as morphological characters are concerned my statement "I have not been able to find any constant morphological differences that will separate *Crinia insignifera* from *Crinia signifera* was based on approximately 20 individuals from Western Australia and more than a thousand living and preserved individuals from Eastern Australia. This lack of morphological differentiation between the eastern and western forms should not be unexpected by those familiar with the literature on these frogs. H. W. Parker had previously found no specific difference between eastern and western forms after a careful examination of more than 400 specimens. Parker's opinion was certainly independent of mine, it was obviously uninfluenced by any knowledge of the behavior of these forms when crossed, and hence is of greater value in reaching the conclusion of morphological identity. When a herpetologist of his competence is unable to find constant differences between the two populations, I think for all practical purposes we can assume they are the same morphological species. It matters not one bit if some future work establishes that the two differ morphologically in some slight though constant way. It is perfectly clear that they are different, though not in ways easily discernible with the superficial methods that are usually adequate in herpetological systematics.

Perhaps some of Rabb and Mosimann's misgivings arise from a misunderstanding of how final and complete I regard the opinions expressed in my paper. Let me say that I certainly do not consider the *Crinia signifera* question to be solved. These frogs present a variety of problems, some of which cannot be answered even with an endless amount of study of preserved material. I performed some experiments that can help to answer some of the questions, while at the same time they raised even more. Perhaps some day I shall be fortunate enough to return to the land where Crinia is found and try to answer a few more.

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April 24, 1956

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THE SIGNIFICANCE OF DIFFERENCES BETWEEN GENOTYPIC FREQUENCIES AND PHENOTYPIC FREQUENCIES

The comment by Sanghvi (1955) on my critique (Glass, 1954) of his data for seven genetical characters in endogamous groups in Bombay (Sanghvi and Khanolkar, 1952) is most interesting, and brings out strikingly the smallness of the effect of inbreeding on the gene frequencies even when the inbreeding coefficient is relatively high (.01). Of course, in small isolates such as the Dunker community in Franklin County, Pennsylvania, studied by Glass, Sacks, Jahn, and Hess (1952), the coefficient of inbreeding may be

considerably higher, and one must keep in mind the generality of isolates of all existing sizes. In the Dunker community, for example, F (Wright's coefficient of inbreeding) was estimated to be .0254 and might be higher. Yet even here, for a gene frequency of .50, the percentage of the recessive homozygotes would amount only to 25.63% instead of 25.0%. It is therefore quite true, as Sanghvi has pointed out, that in the case of common alleles the difference is of no great significance

I regret that Sanghvi's note was not brought to my attention until after its publication, as otherwise I might have discovered sooner the error which led me to state (Glass, 1954) that the statistical significance of the differences between the MN phenotypic frequencies in different endogamous groups was reduced when one converted the data into genotypic frequencies. Checking my original calculations, I find that in shifting from phenotypic frequencies to genotypic frequencies I failed to double the sample size. Sanghvi is therefore quite correct about the increased, rather than decreased, significance which results when the conversion is made.

This leads to the rather amusing conclusion that Sanghvi has supported my original point, namely, that genotypic rather than phenotypic frequencies ought to be used whenever possible, with a better reason than the one I advanced myself. The loss of a degree of freedom in making the conversion may bring out statistically significant differences that are obscured in the crude data.

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DATURA RESEARCH MATERIAL AVAILABLE

The Smith College Genetics Experiment Station was discontinued at the end of 1955, a year after the death of Dr. Albert F. Blakeslee, its founder and director since 1942. For many years the investigations of Dr. Blakeslee and his colleagues at Smith College, and earlier at the Department of Genetics of the Carnegie Institution of Washington, had resulted in the announcement of many new facts and principles resulting from new chromosomal varieties

of Datura with duplicated chromosomes or chromosome sections. However, there are many unfinished research problems and opportunities for investigations with Datura in genetics, cytogenetics, plant physiology and morphology. The ten herbaceous species of Datura provide an excellent opportunity to study many angles of the species problem: hybridization, compatible and incompatible crosses, the barriers to crossability. Tetraploid, as well as diploid lines of most species as well as chromosomally different races are available. In *Datura stramonium* there are available many 2n + 1 types, nearly a hundred different chromosomal races (Prime types), as well as many gene types. Some races have been maintained by selfing for more than forty generations. The National Science Foundation has recently made a grant to Smith College to finance the assembling of the data on Datura genetics and related problems, and its publication in a monograph on Datura. This will be in charge of Amos G. Avery, and the principal contributors will be Dr. Sophie Satin, and Dr. J. Rietsema.

Datura is almost an ideal plant for research. It is easy to grow either in the greenhouse or field; selfing and crossing is simple and a large number of seed is produced. As many as four generations a year have been obtained in special instances although two or three are usual. It is also readily propagated by cuttings or grafting.

Seed of all the species and of most of the races and types have been grown and placed in controlled cold storage. These are available to any investigator who desires to continue some phase of the Datura research. Application should be made to Dr. H. H. Plough, Amherst College, Amherst, Massachusetts indicating the seeds desired and the general nature of the investigation planned. Seeds will be mailed promptly.

Committee of the Genetics Society
of America for the Preservation of
A. F. Blakeslee's Datura material:

H. H. PLOUGH, *Chairman*
R. E. CLELAND
M. DEMEREC
P. C. MANGELSDORF
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